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Evaluation of 11 cycles of reciprocal recurrent selection in BSSS and BSCB1 maize populations

by

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GENERAL INTRODUCTION

The development of superior inbred lines for use as parents of hybrid cultivars has been a major concern of maize (Zea mays L.) breeders. The traditional breeding method in the beginning years of inbred line development was to self pollinate individual plants from open-pollinated cultivars for several generations before testing the lines for their combining ability. As hybrid breeding programs expanded, crosses between elite inbred lines were selfed to produce second-cycle lines. However, hybrids of the second-cycle lines were not remarkably superior to the hybrids of the first-cycle lines. The failure of continued selection in this small group of superior lines was related to restriction of the range of genetic variation imposed by the parents and the rapid approach to homozygosity which limited opportunities for selection.

Early generation testing was one of the first attempts to overcome these objections (Jenkins, 1940; Sprague, 1946). The scheme was used to identify superior genotypes in the early stage of inbreeding by testcross evaluation of S_0 plants. The early testing allowed discarding of unpromising lines and concentration of inbreeding and selection on progeny of desirable S_0 plants. The concept of early testing was developed further by intercrossing the selected individuals to form a new population for continued evaluation and selection. This breeding scheme was designated "recurrent selection".

Recurrent selection was developed to improved breeding populations by gradually increasing the frequency of favorable alleles while

maintaining genetic variation in the populations. The basic technique in recurrent selection is identification of plants with superior genotypes in the source populations, and subsequent intermating of these selected individuals to form a new population. For traits with low heritability, progeny testing may be needed to evaluate the breeding value of the parents.

Recurrent selection can be used for parallel improvement of two populations. The method, now called reciprocal recurrent selection, was proposed by Comstock et al. (1949) to capitalize on both general and specific combining ability. Several studies have shown that reciprocal recurrent selection is efficient in improving mean performance of population crosses. The simultaneous selection in two populations results in complementary improvement in allelic frequencies between populations as evidence by the fact that heterosis in the population crosses is increased with cycles of selection. In most cases, rate of response in grain yield in the population cross is greater than that in the populations per se. This limitation in the rate of response is likely to be influenced by random genetic drift due to finite population size. The effects of genetic drift may cause fixation of undesirable alleles, loss of favorable alleles, and decreasing genetic variation of the populations. The effects of genetic drift may not be avoided in the recurrent selection programs because a limited number of individual are selected for recombination. However, the effects of genetic drift can be minimized by using larger effective population sizes.

Reciprocal recurrent selection has been conducted by the Cooperative

Federal-State maize breeding program in Iowa since 1949 with two synthetic cultivars, 'Iowa Stiff Stalk Synthetic' (BSSS) and 'Iowa Corn Borer Synthetic No. 1' (BSCB1). The objectives of this study were to: (1) determine the direct and indirect response of selection by evaluating performance of population crosses and populations per se, respectively, (2) evaluate the performance of testcrosses of populations with related and unrelated inbred testers, (3) partition the response to selection into that due to additive and dominance gene effects, and (4) evaluate the effects of genetic drift on the response to selection.

LITERATURE REVIEW

The definitive goal of most maize breeding programs is the development of superior inbred lines for use in commercial hybrids. The standard system of inbred line development initially involved selection of desirable plants from heterogeneous populations and inbreeding progenies of these plants to homozygosity in combination with selection among and within progenies. Superior lines that combine well were used in the production of commercial hybrids. As hybrid breeding programs developed further, there was an increasing tendency to use second-cycle lines derived from segregating generations of crosses between superior inbred lines. However, their hybrids were not remarkably superior in yield to the hybrids of the first-cycle lines. This standard system of line development has been criticized as being inefficient mainly because of two reasons:

1. the rapid approach to homozygosity may not allow adequate opportunity for selection to increase the frequency of favorable alleles. Thus, random fixation of alleles will occur during the inbreeding process, and
2. the performance level of inbred lines is set by the genotype of the foundation plant and may restrict the range of genetic variation available for selection.

To overcome these limitations, a new approach was needed that maintain genetic variation in the breeding population while allowing incremental change in the frequency of desirable alleles by intermating lines derived from selected plants. These logical ideas were developed

into a breeding scheme in the 1940s and designated "recurrent selection".

Recurrent selection theoretically causes small changes in genetic variation in a population as a result of selection pressure imposed. Also, the rate of inbreeding can be reduced by modifying the numbers of selected plants intermated in each cycle. Recurrent selection is usually conducted in parental populations that have a broad genetic base.

Methods of Recurrent Selection

Recurrent selection can be defined as a method of breeding designed to gradually combine the most favorable alleles contained in a group of foundation plants into a single plant by selecting among the progeny of each generation produced by intermating the selected plants (or their self progeny) of the previous generation (Allard, 1960). The cyclical process of progeny development, progeny evaluation, and intermating of the superior progenies to form a new population for the next cycle of selection is conducted in a repetitive manner (Hallauer and Miranda, 1988). Cyclical selection will gradually increase the frequency of favorable alleles in an improved population, thus, enhancing the probability of obtaining superior individuals. Theoretically, the recycled populations will contain genetic variation for additional cycles of selection.

Source populations for recurrent selection can be set up in various ways depending on resourcefulness of the breeder. A source population can be an open-pollinated variety, a synthetic variety, or a hybrid. Hallauer and Miranda (1988) suggested that a source population should

have adequate genetic variation, a high mean, and exhibit heterosis in crosses. Improved populations resulting from recurrent selection can be used as a source of germplasm suitable for the extraction of superior inbred lines for producing hybrids, as parents of synthetic varieties, as improved populations per se, or as parents of a population cross.

Allard (1960) and Sprague (1967) classified the various recurrent selection methods into two broad categories: phenotypic recurrent selection and genotypic recurrent selection. The selection unit for phenotypic recurrent selection is an individual plant. The effective use of this method is restricted to characters with sufficiently high heritability that a phenotypic evaluation can be made by visual inspection or by simple measurement. Genotypic recurrent selection basically applies to all breeding schemes where some form of progeny testing is done to determine the breeding value of individual plants.

Three main types of genotypic recurrent selection have been recognized: recurrent selection for general combining ability (GCA), recurrent selection for specific combining ability (SCA), and reciprocal recurrent selection (RRS). These recurrent selection schemes differ from each other mainly in the type of testcrosses used to measure combining ability. General combining ability (GCA) was defined by Sprague and Tatum (1942) as the average performance of a line in hybrid combinations. They defined specific combining ability (SCA) as the deviation from performance of a specific hybrid combination predicted on the basis of GCA. The differences in GCA are mainly due to additive genetic variance and differences in SCA are attributable to non-additive genetic variance.

Different genotypic recurrent selection methods were developed primarily as a result of different concepts of the types of gene action considered to be of greatest important in the expression of grain yield in maize. Proposals similar to recurrent selection were first suggested by Hayes and Garber (1919) and East and Jones (1920) (Sprague, 1952). However, these proposals did not lead to the use of recurrent selection. It was not until 1940 that Jenkins described in detail a selection scheme, that later became known as recurrent selection for GCA. The scheme was developed as a direct result of his experiment with early generation testing for developing synthetic populations in maize. Jenkins (1935) proposed early generation testing based on the assumptions that the combining ability of a line was established early in the inbreeding process. A selected S_0 or S_1 plants judged on combining ability test offers superior lines on selfing, while early discarding of unpromising lines. The basic procedures of Jenkins' breeding scheme for one cycle of selection were as follows: 1) self and cross S_0 plants to a heterozygous tester; 2) evaluate the testcrosses in replicated yield trials and make selection based on testcross performance; and 3) intermate the selected S_1 lines in all combinations to produce the improved population. The procedure is repeated and subsequent cycles of selection are conducted in the same manner.

Hull (1945) proposed a modification of Jenkins' breeding scheme and designated his scheme recurrent selection for SCA. His method was designed to determine differences in specific combining ability by testcrossing S_0 plants or S_1 lines with a homozygous tester.

The chief point of difference between the two breeding schemes arose from the debate on the type of gene action controlling heterosis in maize hybrids. Jenkins supported the "dominant hypothesis of heterosis" which explains hybrid vigor as a function of the number of dominant favorable alleles contributed by each parent. Hull, however, argued that overdominant gene action was of greater importance. He supported the hypothesis that heterosis results from overdominance and/or the interaction of genes at different loci (epistasis). Thus selection should be emphasized for specific combining ability to develop a complementary population with allelic frequencies divergent from those in the inbred tester. By Hull's scheme, the frequency of heterozygotes would be increased in hybrids between lines derived from population and the inbred tester.

Comstock et al. (1949) suggested a breeding scheme that will, with certain limitations, capitalize on both general and specific combining ability. The scheme, now called reciprocal recurrent selection, was designed to exploit all types of gene action. Moreover, RRS eliminates one objection to the previous recurrent selection schemes because selection is practiced in two populations simultaneously instead of one. RRS improves two genetically diverse populations, A and B, simultaneously on the basis of performance of crosses between the populations. The details of the procedure are as follows:

1. Season one: self and cross a number of plants (i.e., 200) from population A to four or more random plants in population B. Similarly, a number of plants from population B are selfed and

crossed to four or more random plants in population A.

2. Season two: evaluate the two sets of testcross progenies in replicated yield trials and select the best on the basis of testcross performance from each population.
3. Season three: intermate the S_1 progenies derived from the selfed seed of the superior S_0 plants from population A. The selected S_1 progenies from population B are intermated in the same manner to form an improved population.
4. Conduct the subsequent cycles of selection in the same manner as described for step one to three by using the improved population.

Comstock et al. (1949) point out that regardless of the type of gene action involved in heterosis, RRS would be at least as effective as the other recurrent selection methods in improving population cross performance.

Recurrent selection methods are also divided into two broad groups: intrapopulation recurrent selection and interpopulation recurrent selection. Intrapopulation recurrent selection is used to improve the source population, whereas interpopulation recurrent selection emphasizes selection in the cross between two source populations. Since the ultimate goal in most modern maize breeding programs is superior hybrids, expression of heterosis should be considered for both intra- and inter-population improvement programs. Simultaneous improvement of two heterotic source populations seems to be a reasonable approach. However, intrapopulation selection has also been effective for developing lines

that when crossed to elite lines produced high-performance hybrids. A complete description of recurrent selection methods in maize was given by Hallauer and Miranda (1988).

Theoretical Aspects of Reciprocal Recurrent Selection

A number of theoretical investigations have been made to compare reciprocal recurrent selection schemes with other recurrent selection schemes. Comstock et al. (1949) provided theoretical comparisons of recurrent selection for GCA, recurrent selection for SCA, and RRS. Limits to improvement as well as rates of improvement were evaluated using different types of gene action. When limits to improvement were evaluated, three conclusions were found. First, with partial dominance, the improvement limit was approximately the same for recurrent selection for GCA and RRS. Recurrent selection for SCA would have the same maximum limit only when favorable alleles present in the selection material were also present in the tester line. Second, the improvement limits for recurrent selection for SCA and RRS were equivalent and superior to recurrent selection for GCA as overdominance becomes more important. Finally, with complete dominance all three methods attained the same limits to improvement. However, recurrent selection for GCA would be less efficient if the tester was homozygous for the favorable allele at a large number of loci.

Three conclusions were also listed when relative rates of improvement were considered. For complete or nearly complete dominance, RRS showed an increasing advantage over the other two methods in initial

cycles. However, recurrent selection for GCA provided the fastest rate of improvement with further cycles of selection. With partial dominance, the rate of improvement was the same as for the complete dominance condition but the initial advantage for RRS was not as great and recurrent selection for GCA would probably show a slight advantage. Finally, recurrent selection for GCA would provide the fastest rate of improvement in the long term if the tester used in recurrent selection for SCA had a low frequency of favorable alleles. Comstock et al. (1949) generally concluded, in accordance with their theoretical anlaysis, that overall RRS was as effective as the other two methods under the wide range of genetic conditions considered.

Cress (1966) presented a general formula for comparing the rate of progress from RRS with selection within the two original populations (WPS). He showed that for all positive dominance relationships, WPS, which may be expected to use mostly GCA had a rate of progress greater than or equal to RRS when $a_1 + b_1 > 1.0$, where a_1 and b_1 are the frequency of the favorable dominant alleles in original populations. The progress by RRS was greater than WPS when $a_1 + b_1 < 1.0$. The results indicated that for partial to complete dominance the rate of progress from RRS would be superior to WPS for only a few cycles if selection was effective in increasing the frequency of favorable dominant alleles.

Cress (1966) suggested that the relative performance of RRS compared to WPS was due to the magnitude of additive genetic variance in both original populations compared to additive variance in the testcross progenies. When $a_1 + b_1 > 1.0$, the relative amounts of additive variance

within the populations is greater than the additive variance of the testcross progenies. Thus, the rate of progress for WPS is greater than for RRS. Genetic divergence between two populations is not an essential requirement for increasing the rate of progress of RRS, and the rate of progress is dependent only on the additive genetic variance among the testcrosses. In general, genetic divergence may decrease the additive genetic variance among the testcrosses.

When hybrid performance was considered, Cress (1966) pointed out that RRS should be effective for obtaining elite hybrids. WPS would be an ineffective method for developing elite hybrids when overdominant gene action and certain allelic frequencies prevailed.

Cress (1967) used computer simulation to study the change in the means of parental and hybrid populations with RRS. The methods investigated by simulation were RRS as proposed by Comstock et al. (1949) and two modifications of RRS. The first modification required one generation of selfing at the beginning of each cycle of selection before producing the testcrosses (RRS_s). The second modification was to retain the original populations as a constant tester (RRS_c). Purely overdominant and completely dominant models were used for each of a given set of starting allelic frequencies in the original populations. Twenty cycles of continuous selection were conducted for each method. Each simulated population was composed of 90 individuals and the 10 best individuals from each population were used to form the new populations for next cycle. Each quantitative trait was controlled by more than 40 loci. For the complete dominance model, gain in the hybrid population was

approximately equal for all three methods after 20 cycles of selection. However, gain during the first few cycles was greater for the RRS_s method. None of the methods were effective at increasing the means of the populations per se. With overdominance, the RRS and RRS_s methods displayed good response for the hybrid population, but the RRS_c method showed little or no improvement in hybrid performance. Hybrid performance could be improved in overdominance model only when the two populations were improved complementary to each other to allow increases in the amount of additive genetic variance in the population cross. Complementary improvement is not possible when a constant tester is used as with the RRS_c method.

Cress (1967) indicated that the improvement in populations per se, depends on the covariance between additive effects of alleles in hybrid and in the populations per se. For partial and complete dominance, covariances for both populations are always positive, and consequently, genotypic value of the populations increase. With overdominance, increases in genotypic value of the parental populations depend on the distance from the equilibrium allelic frequency. If the frequencies of the alleles in populations are on opposite side of the equilibrium value, the covariance for both populations is negative, and consequently, means of the populations will decrease. On the other hand, population means will increase if the allelic frequencies of both populations are on the same side of the equilibrium value. The increase is continued until the allelic frequency in one of the populations crosses to the opposite side of the equilibrium value and both populations will show a decrease in

their means in subsequent cycles of selection. The point where one of the populations passes the equilibrium value will determine the maximum mean for both populations. According to this study, Cress stated that the short term increase in population per se means in RRS cannot be interpreted as the presence for a predominance of partial or complete dominance.

Cress (1967) also demonstrated specific effects of RRS on the two populations. Although RRS emphasizes hybrid performance, selection pressure is also exerted on the two closed populations. For a single locus with no overdominance, the selection pressure in each of the two populations will be equal only when the allelic frequencies in both populations are the same. Otherwise, the population with the lowest allelic frequencies will have the lowest selection pressure. Consequently, the population with the lowest allelic frequencies immediately reaches an equilibrium value below its maximum genetic potential where random drift can cause chance fixation of the alleles. When many loci are taken into account, the maximum genetic potential for both populations cannot be attained because of either finite population size that causes drift from equilibrium allelic frequencies or completely dominant gene action.

A theoretical investigation of the efficiency of alternative breeding methods for improving the cross between two populations was made by Hill (1970). The methods considered were pure line selection (PLS), recurrent selection with an inbred tester (RST) as proposed by Hull (1945) and RRS. Comparisons were made in each selection method using the

same selection limits with specified levels of dominance, assuming no epistasis, linkage equilibrium and two alleles per locus. The selection limit was defined as NS, where N is the effective population size and S = ia/σ_f, where i is the standardized selection differential, a is effect of an allele on the trait, and σ_f is the standard deviation of progeny means. Finite population size was introduced so that the defined selection limit was the expected limit rather than maximum limit possible with fixation of only favorable combinations. The other benefit of using the finite model was that it was required for the study of initial equilibrium with overdominant gene action. The analysis showed that with complete dominance and low allelic frequency RRS was more effective than PLS, and RST was the poorest method. However, the efficiency of RST depended on the initial allelic frequencies in the two strains. For higher initial allelic frequencies, RST may have similar efficiency as RRS. The rates of improvement were similar for RRS and PLS with partial dominance but RST was less efficient, especially at high values of the selection limit. With overdominance and initial equilibrium in each population, PLS was not a useful breeding method. For alleles with small effect, the total improvement up to cycle t was proportional to F_t^2 with RRS and F_t with RST and the rates of responses were proportional to $F_t(1-F_t)$ and $1/2(1-F_t)$ respectively, where F_t is the inbreeding coefficient at the beginning of the program. Thus, RRS and RST were predicted to give approximately the same rate of improvement, and the greatest rate could be obained when F_t = 0.5. Because of the assumptions, the analysis will be of limited value if heterosis is taken into account, because epistasis may be an important

factor contributing to heterosis in some cases. Nevertheless, Hull (1970) concluded that with particular exceptions RRS was generally superior to other selection methods.

Dickerson (1952) also made theoretical comparisons of the efficiency of the alternative selection methods. He pointed out in his review that recurrent selection with a highly inbred tester could show higher initial response than RRS because there was no unstable equilibrium state.

Population sizes has been considered an important factor in the long term improvement of populations undergoing recurrent selection. Theoretically, selection within infinitively large populations is expected to increase the frequency of favorable alleles until the alleles eventually become fixed. Typically, populations used in selection programs are of finite size and some favorable alleles may be lost by genetic drift so that the maximum genetic potential may never be attained. Robertson (1960) emphasized the problems of selection limits in finite populations. He indicated that some favorable alleles may be lost by chance during the selection process, so that the final progress depends on the effective population size, the initial allelic frequencies, and the effects of alleles. Average rates of progress from selection are also influenced by population size.

Comstock (1977) stated that effective population size in any recurrent selection program should be sufficient to overcome the ultimate consequences of genetic drift. Also, Hill (1970) pointed out that initial progress would not be made in a RRS program if the breeding populations were finite and alleles with heterozygote superiority were

initially at equilibrium.

Selection Responses in Reciprocal Recurrent Selection

Estimates of progress from continued selection are one of the most important considerations for a plant breeder who needs to verify the effectiveness of a given selection program or compare the relative efficiency of different breeding systems. There are several approaches for estimating the realized progress from selection, which in most cases, involves a regression model.

Eberhart (1964) suggested a regression model for estimating the rate of response to recurrent selection program by regressing the observed means of the selected populations and their crosses on cycles of selection. The linear regression coefficient from the model, which provides the rate of gain per cycle of selection, is estimated by using least squares regression analysis described by Anderson and Bancroft (1952) or Steel and Torrie (1980). The analysis also partitions the sums of squares among populations into linear, quadratic, and deviations from regression. If deviations from linear regression are not significant, the linear regression coefficient from the model is an estimate of gain per cycle. Eberhart (1964) also proposed another model and analysis that are used to compare progress among different methods of recurrent selection conducted in a common base population.

According to Smith (1979a), least squares regression analysis estimates changes in the population means but does not show directly the effect of changes in allelic frequencies in the populations. Moreover,

changes in the population means due to increases in the favorable allele frequencies may be biased by the effects of inbreeding depression due to finite population size. Smith (1979a, 1979b) developed statistical models for evaluating progress from selection by relating changes in the population means to changes in allelic frequency and inbreeding depression due to finite population size. He reported that with little or no overdominance, finite population size may cause a decrease in frequency or loss of favorable alleles and therefore limit the progress from selection.

Several studies on reciprocal recurrent selection have been conducted and the results have been periodically reported in literature.

Thomas and Grissom (1961) reported on the effectiveness of RRS to improve mean grain yield, popping volume, and lodging resistance in two popcorn populations. Selection of lines for intermating in each cycle was based on a weighted system where yield and popping volume were given twice the weight of lodging resistance. They reported that all three traits were improved after two cycles of selection.

Douglas et al. (1961) reported results of two cycles of RRS for grain yield in two varieties of maize, 'Yellow Surcropper' and 'Ferguson's Yellow Dent'. Yield of Ferguson's Yellow Dent population was improved at a rate of 10% per year while no consistent improvement was made in Yellow Surcropper populations. Average response in the population cross was 5.8% per year. They concluded that the increase in yield of the population cross was due to increased combining ability in Yellow Surcropper composite.

Results of three cycles of RRS and intrapopulation full-sib family selection involving two North Carolina open-pollinated varieties, 'Jarvis' and 'Indian Chief', were reported by Moll and Robinson (1966). Grain yield after three cycles of RRS increased 4.3%, 1.7%, and 0.8% per cycle in Jarvis, Indian Chief, and Jarvis x Indian Chief, respectively. Heterosis in the population cross was increased by the RRS but unchanged by full-sib selection.

Moll and Stuber (1971) subsequently reported on the effectiveness of six cycles of both selection methods. The responses by RRS were 2.3%, 1.2%, and 3.5% per cycle for Jarvis, Indian Chief, and the population cross, respectively. Response of both varieties to full-sib selection were 2.1 times greater than their response to RRS while response of the variety cross to RRS was 1.3 times greater than the response to full-sib selection. Mid-parent heterosis in the variety cross increased 9.5% for RRS but decreased 3.8% for full-sib selection. Increases in yield were generally associated with increases in tillers and ears per plant and decreases in plant and ear heights.

Similar responses were observed after eight cycles of RRS and full-sib selection (Moll et al., 1978). Heterosis was incressed 11.3% after RRS and decreased 2.1% after full-sib selection. The contrasting effects observed for changes in heterosis in the two selection methods as well as increases in the means of populations per se by RRS were interpreted as indicating that dominant gene action was more important in these populations than overdominant gene action.

After 10 cycles of RRS, Moll and Hanson (1984) reported that the

rate of improvement in grain yield was 2.4% and -0.3% per cycle for Jarvis and Indian Chief, respectively, and 2.7% per cycle for Jarvis x Indian Chief. However, after the eighth cycle of selection no change in response was observed. The populations and their cross showed increased ears per plant but the increase was greatest in the Jarvis population which initially had fewer ears per plant than the Indian Chief population. For grain yield, the rate of improvement for crosses of the selected populations to the original populations was not one-half of that for the corresponding selected populations per se. This supported results from previous studies that the improvement involved alleles with dominance effects. Diversity analysis (Hanson and Casas, 1968; Hanson, 1983) obtained from diallel information was conducted to evaluate genetic changes within populations. The analysis showed that response to selection for yield and ears per plant involved both additive and dominance effects. However, additive effects were more important than dominance effects for ears per plant. The Jarvis population provided greater divergence for both yield and ears per plant than that found in the Indian Chief population. The divergence within Jarvis was primarily attributed to additive gene effects whereas divergence within Indian Chief resulted from additive and dominance gene effects. Moll and Hanson (1984) concluded that RRS utilized the additive effects from Jarvis and dominance effects from Indian Chief to create divergence. They also suggested that the cumulative effects of inbreeding depression may be involved in the lack of response observed after the eighth cycle, and may have contributed to the increased divergence of the populations per se.

Darrah et al. (1972) evaluated two cycles of RRS in Kenya using 'Kitale II' (KII) and 'Ecuador 573' (Ec 573) varieties as base populations. Increases in yield were 0.6 q/ha, 3.0 q/ha, and 3.3 q/ha per year for KII, Ec 573, and KII x Ec 573, respectively. After three cycles of selection, Darrah et al. (1978) reported gain per year of 2.09 q/ha in the variety cross and 0.97 q/ha in Ec 573 variety whereas a slight decrease in yield was obtained in KII variety. Increased yield was accompanied by increases in ears per 100 plants. After five cycles of selection, Darrah (1985) reported that the variety cross had a significant increase in yield of 1.75 q/ha per year (5.5% per cycle) but neither varieties showed a significant response for yield. He also found that yield improvement in the variety cross was associated with an increase in the number of usable ears and a decrease in lodging and days to flowering.

Brown and Allard (1971) evaluated the genetic effects of RRS for yield of two maize populations. Nine isozyme loci were used to monitor the changes in genetic effects caused by RRS. Yields of populations and population crosses were successfully improved by two cycles of selection. It appeared from the results of the isozyme study that the genetic structure of the populations was not modified by RRS. In addition, the slight shifts in allelic frequency at most of the isozyme loci considered may be explained by random genetic drift.

Gevers (1975) compared three cycles of RRS in the popultions 'Teko Yellow' and 'Natal Yellow Horsetooth' based on two methods of sampling the S_0 plants before crossing. When random S_0 plants were sampled, yield

increased 7.5%, 7.4%, and 5.8% per cycle in Teko Yellow, Natal Yellow Horsetooth, and the population cross, respectively. The rates of gains were 7.1%, -0.5%, and 3.3% per cycle in Teko Yellow, Natal Yellow Horsetooth, and the population cross, respectively, when S_0 plants were selected for agronomic traits. They concluded that gains in yield were greater when random rather than selected S_0 plants were used for selfing and crossing in RRS program.

Conti et al. (1977) reported that two cycles of RRS in two Italian maize populations resulted in yield increase of 7.5% per cycle in the population cross. An increase in yield of 3.9 and 2.0 q/ha per cycle were observed in parental populations.

Paterniani and Vencovsky (1977) modified RRS by testcrossing half-sib families. Observed responses after one cycle of selection were 7.5%, 3.5%, and 7.5% per cycle for the Cateto population, Piramex population, and population cross, respectively. Paterniani and Vencovsky (1978) also reported a significant increase in grain yield of 2.5% per cycle in the population cross after three cycles of their second modification of RRS in Dent Composite and Flint Composite populations.

A RRS program in Iowa was initiated with the synthetic varieties, 'Iowa Stiff Stalk Synthetic' (BSSS) and 'Iowa Corn Borer Synthetic No. 1' (BSCB1). Results from the first four cycles of selection were reported by Penny and Eberhart (1971). They found significant increases in yield of 1.38 q/ha (2.5%) and 1.18 q/ha (1.8%) per cycle in BSSS and BSSS x BSCB1 populations, respectively. Yield of BSCB1 decreased slightly at the rate of 0.64 q/ha (1.1%) per cycle.

An intensive evaluation after five cycles of the RRS was conducted by Eberhart et al. (1973). Progress for yield of the population cross was 2.73 q/ha (4.6%) per cycle, whereas the populations per se showed a slight increase of 0.24 q/ha (0.4%) and 0.47 q/ha (0.9%) per cycle for BSSS and BSCB1, respectively. Changes in yields of the populations and population cross were associated with increases in ears per 100 plants and decreases in stalk lodging. Plant height decreased slightly in the populations but increased slightly in the population cross. Increased heterosis in the population cross and lack of progress in parental populations could partly be explained by inbreeding which was approximately 22% by the fifth cycle of selection. Eberhart et al. (1973) concluded that overdominant (or pseudo-overdominant) gene action must be relatively important for yield because there was improvement in the population cross without improvement in the parental populations and because there was a lack of improvement of topcrosses to an unrelated tester.

Martin and Hallauer (1980) reported progress after seven cycles of selection in the same RRS program. The population cross showed an increase in yield of 1.75 q/ha (3.0%) per cycle. A slight increase in yield of 0.6 q/ha (0.7%) and 0.57 q/ha (1.2%) per cycle were observed for BSSS and BSCB1, respectively. Heterosis increased from 14.9% to 41.7% in the population cross. Genetic variance for grain yield estimated from testcross yield trial data showed no change after seven cycles of selection.

Results of eight cycles of RRS in BSSS and BSCB1 were reported by

Smith (1983). The response from selection was evaluated separately for cycles 0-4 and cycles 4-8. The averaged response in yield over all cycles of BSSS x BSCB1, BSSS, and BSCB1 was 3.1%, 1.9%, and 0.6% per cycle, respectively. Rate of improvement for yield of the population cross increased 46% from 2.47 q/ha per cycle for cycles 0-4 to 3.61 q/ha per cycle for cycles 4-8. The populations BSSS and BSCB1 also showed greater response in cycles 4-8 than in cycles 0-4. The increases in responses were attributed to two changes made after the fourth cycle of selection. First, S_1 plants rather than S_0 plants were used to make the half-sib progenies and, secondly, the use of machine harvesting of the yield trials rather than hand harvesting. Heterosis in the population cross after eight cycles of selection increased from 22.6% to 31.5% (Hallauer, 1985). Because only 10 lines were recombined in each cycle, the lack of response in parental populations may be due to drift. Smith (1983) showed that the response of parental populations adjusted for the effects of genetic drift were greater than the direct response estimated from population cross.

Explanation of Thesis Format

This dissertation includes two sections. Section I includes a study of the direct and indirect responses to reciprocal recurrent selection in BSSS and BSCB1 maize populations and evaluation of the changes in inbreeding depression and heterosis with cycles of selection. Section II includes an evaluation of the contribution of additive and dominance gene effects to the gain from selection, and estimation of effects due to

genetic drift and selection on the changes in mean of the populations.

Each section is in the form of a manuscript that will be submitted to a professional scientific journal. A General Discussion and Conclusions follow Section II. Appendix is presented at the end of the dissertation. This appendix will not be included in the published manuscript.

SECTION I. DIRECT AND INDIRECT RESPONSES TO RECIPROCAL RECURRENT SELECTION IN BSSS AND BSCB1 MAIZE POPULATIONS

ABSTRACT

Improvement of a germplasm base for use as a parental source for developing inbred lines has been an important part of most maize (Zea mays L.) breeding programs. Reciprocal recurrent selection is a cyclical breeding procedure designed to improve two broad-genetic base populations simultaneously. The objective of this study was to evaluate the direct and indirect response of 11 cycles of reciprocal recurrent selection in BSSS(R) and BSCB1(R) maize populations. The populations per se, populations per se selfed, interpopulation crosses, and interpopulation crosses selfed corresponding to C0, C4, C7, C8, C9, C10, and C11 cycles of the populations were evaluated. Testcrosses of respective cycles of the populations per se with inbred lines B73 and Mo17, and testcrosses of C0, C4, C7, C9, and C11 cycles of populations with BSSS(R)C0 and BSCB1(R)C0 were included in the study.

Response in grain yield of BSSS(R)Cn x BSCB1(R)Cn population crosses was 6.95% (0.28 Mg ha^{-1}) $cycle^{-1}$. Grain yield of the BSCB1(R)Cn increased 1.94% (0.06 Mg ha^{-1}) $cycle^{-1}$ but grain yield of the BSSS(R)Cn did not change significantly. Midparent heterosis increased from 25.44% for the C0 x C0 population cross to 76.04% for the C11 x C11 population cross. Inbreeding depression in the population crosses increased from 1.01 Mg ha^{-1} to 2.32 Mg ha^{-1} after 11 cycles of selection. It was concluded that heterozygous loci involving grain yield in the population crosses would have increased with cycles of selection.

Testcrosses of the populations to the C0 populations and the inbred lines showed linear increases in grain yield in most cases indicating

that selection improved general as well as specific combining ability of the populations. Selection was effective in reducing root and stalk lodging. No changes in grain moisture were observed. Changes in other agronomic traits were in the desired direction.

INTRODUCTION

Recurrent selection is a cyclical selection procedure designed to improve quantitatively inheritated traits in the population. Theoretically, continued selection will gradually increase frequency of favorable alleles within the improved population and, therefore, increase the chances of obtaining superior individuals from the population. The population is expected to be improved without reducing genetic variability so that additional improvement can occur in the future cycles.

A recurrent selection scheme designed to improve the cross between two populations is known as reciprocal recurrent selection (RRS). RRS was originally proposed by Comstock et al. (1949). The selection method was designed to exploit both additive and non-additive genetic effects. Improvement of the cross by complementary improvement in two parental populations seems to be a logical approach for maize breeding programs where hybrids are the final product of selection (Hallauer, 1987).

RRS has been conducted by the Cooperative Federal-State maize breeding program in Iowa since 1949 with two synthetic cultivars, Iowa Stiff Stalk Synthetic (BSSS) and Iowa Corn Borer Synthetic No. 1 (BSCB1). Several studies (Penny and Eberhart, 1971; Eberhart et al., 1973; Martin and Hallauer, 1980; Smith, 1983; Helms et al., 1989) with these populations have shown that RRS has been effective for improving the population cross (direct response). However, the populations per se have shown inconsistency in their responses to selection.

The objective of this study was to determine the response after 11

cycles of RRS in BSSS(R) and BSCB1(R) populations by evaluating population cross performance (direct response), parental populations per se (indirect response), and their crosses with related and unrelated testers.

MATERIALS AND METHODS

The two synthetic varieties used for initiating the RRS program in Iowa were BSSS and BSCB1. BSSS was developed by intercrossing 16 lines selected for good stalk quality (Sprague, 1946). BSCB1 was synthesized from 12 lines which had resistance to leaf feeding by the first generation European corn borer (Ostrinia nubilalis Hübner) (Hallauer et al., 1974). The details of the RRS procedure through cycle 5 were described by Penny and Eberhart (1971). Several changes have been made in the selection program since the initiation of the program in 1949. After the fifth cycle, S_1 plants rather than S_0 plants were used to make the half-sib progenies, and selection of superior progenies was based on machine-harvested grain yield rather than hand-harvested grain yield. Beginning at cycle 8, 20 rather than 10 selected S_1 progenies from the parental populations were intermated to form the next cycle populations. The selection method was changed from half-sib RRS to full-sib RRS after the ninth cycle. Because the populations are not predominantly two-eared, S_1 lines were used to produce the reciprocal full-sib progenies. The procedure was to self a selected plant in a S_1 progeny row of BSSS(R)Cn and cross it to four plants in a S_1 progeny row of BSCB1(R)Cn. A selected plant in the BSCB1(R)Cn row was then selfed and crossed to four plants in the BSSS(R)Cn row that was previously used as a male. The eight cross-pollinated ears were harvested and shelled in bulk to represent a reciprocal full-sib family. Remnant S_1 seed, rather than S_2 seed, of selected families was intermated to form the next cycle population. Approximately 100 testcrosses were evaluated each cycle

except 160 testcrosses were used in cycle 9 and 112 testcrosses were used in cycle 11. The primary trait under selection has been grain yield with selection pressure on less grain moisture at harvest and resistance to root and stalk lodging. Beginning with cycle 9, superior progenies were selected by using a selection index weighted by the heritabilities of grain yield, grain moisture, root lodging, and stalk lodging (Smith et al., 1981a; 1981b).

In the 1987 breeding nursery at the Agronomy and Agricultural Engineering Research Center near Ames, Iowa, a population diallel was produced among the C0, C4, C7, C9, and C11 cycles of BSSS(R) and BSCB1(R). In addition, the C8 and C10 interpopulation crosses of BSSS(R) and BSCB1(R) were produced. Seed of the C0, C4, C7, C8, C9, C10, and C11 of BSSS(R) and BSCB1(R) populations per se, populations per se selfed, and testcrosses of the populations to inbred lines B73 and Mo17 were also produced. Selfed seed of the C0, C4, C7, C8, C9, C10, and C11 interpopulation crosses was produced in the 1988 nursery. The populations per se, populations per se selfed, and interpopulation crossses selfed were produced by intercrossing or selfing approximately 100 plants. The population crosses were produced by reciprocally crossing 50 plants from each population. Testcrosses of the populations to the inbred lines were produced by sampling 50 plants as males or females from the populations.

The noninbred and inbred material were evaluated in separate experiments grown at four Iowa locations (Ames, Ankeny, Martinsburg, and Clarence) in 1988 and 1989. Data were not obtained from the Clarence

location in 1989 due to the residual effects of herbicides used on the soybean [Glycine max (L.) Merrill] crop grown the previous year. The entries included in the noninbred experiment were the 47 population crosses, 14 populations per se, 28 testcrosses, and 14 checks. Duplicate entries of the BSSS(R)C0 and BSCB1(R)C0 populations per se and the C0 x C0, C4 x C4, C7 x C7, C9 x C9, and C11 x C11 interpopulation crosses between BSSS(R) and BSCB1(R) were also included for a total of 110 entries. The 110 entries were evaluated in a 10 x 11 triple rectangular-lattice design. The entries included in the inbred experiment were the 14 populations per se selfed in 1988 and the 14 populations per se selfed plus the seven interpopulation crosses selfed in 1989. The inbred entries were evaluated in a randomized complete-block design with three replications.

Plots were two-rows 5.49 m long with 0.76 m between rows. All plots were overplanted and thinned to a uniform stand. Stand density was approximately 62,190 plants ha^{-1} for the 1988 experiments and 52,600 plants ha^{-1} for the 1989 experiments. All experiments were machine-planted and harvested with no gleaning of dropped ears. Data for grain yield (Mg ha^{-1} at 15.5% grain moisture), grain moisture (%), stand (plants ha^{-1}), stalk lodging (% plants broken below the ear node), and root lodging (% plants inclined more than 30^{o} from vertical) were collected from seven experiments. Ear height (cm) and plant height (cm) were obtained from five experiments. Ear and plant height were calculated as the average of measurements on ten competitive plants per plot and measured as the distance from the soil surface to highest ear bearing

node (ear height) and the node of the flag leaf (plant height). Silking date and pollen date were recorded as the number of days from planting to 50% silk emergence and 50% pollen shed, respectively. Silking and pollen date were recorded at the Ames location in 1988 and 1989.

The analyses of variance for individual environments of the noninbred experiment were calculated according to the analysis for a rectangular lattice. Means adjusted for lattice block effects were used to calculate the combined analysis of variance over environments (year-location combination). All effects in the model were considered fixed except environments. The genotype x environment interaction mean squares were used in all tests of significance among entries. Only the data for the BSSS(R)Cn and BSCB1(R)Cn populations per se; BSSS(R)Cn x BSCB1(R)Cn interpopulation crosses; BSSS(R)C0 x BSSS(R)Cn, BSSS(R)C0 x BSCB1(R)Cn, BSCB1(R)Cn x BSCB1(R)Cn, and BSCB1(R)C0 x BSSS(R)Cn population crosses; and testcrosses of BSSS(R)Cn and BSCB1(R)Cn to the inbred lines B73 and Mo17 are reported in this study.

The populations per se and population crosses were separated into three regression groups based on common C0 genotypes. The three groups were the BSSS(R)Cn populations per se and BSSS(R)C0 x BSSS(R)Cn population crosses; the BSCB1(R)Cn population per se and BSCB1(R)C0 x BSCB1(R)Cn population crosses; and the BSSS(R)Cn x BSCB1(R)Cn, BSSS(R)C0 x BSCB1(R)Cn, and BSCB1(R)C0 x BSSS(R)Cn interpopulation crosses. The sums of squares for each group were partitioned in a manner similar to the procedure of Eberhart (1964). This analysis allowed us to fit the regression lines through the common C0 intercept. Because the C0 and

some of the interpopulation crosses of each group had twice as many observations as the other cycles, weighted least squares was used where the weights were the variances of the cycle means. Standard errors of the regression coefficients were obtained by taking the square root of the appropriate diagonal element of the $(X'W^{-1}X)^{-1}$ matrix, where W is a matrix with the variances of the cycle means on the diagonal and zeros on the off diagonal. The sums of squares for the four testcross groups were partitioned using standard polynomial regression procedures. The linear regression coefficient obtained from regression models with only the linear effect were used as estimates of the average rate of response per cycle. Percentage of response per cycle was calculated as the ratio of the linear regression coefficient to the intercept multiplied by 100.

Analyses of variance for a randomized complete-block design were calculated for each experiment and combined across environments (year-location combination) for the inbred experiment. All effects in the model were considered fixed except environments. The genotype x environment interaction mean square was used in all tests of significance among entries. The sums of squares among the BSSS(R)Cn and BSCB1(R)Cn populations per se selfed and BSSS(R)Cn x BSCB1(R)Cn interpopulation crosses selfed were partitioned using standard polynomial regression procedures.

Estimates of inbreeding depression in absolute units were calculated as the noninbred (S_0) minus the inbred (S_1) generation means. Standard errors of inbreeding depression in absolute units were calculated as the square root of the sum of the variance of inbred and noninbred generation

means (Lamkey and Smith, 1987). Midparent heterosis was calculated as the difference between the mean of a population cross and the average of the two parents. The standard error of midparent heterosis was calculated as the square root of 1.5 times the variance of an entry mean.

RESULTS

Moisture stress occurred during 1988 and 1989 resulting in lower than average yields. The average grain yield over all environments was 5.46 Mg ha^{-1} for the S_0 experiments and 3.05 Mg ha^{-1} for the S_1 experiments. The mean grain yields for the S_0 experiments ranged from 3.13 to 8.39 Mg ha^{-1}, and from 1.90 to 5.47 Mg ha^{-1} for the S_1 experiments. Mean grain yields of single-cross checks, B73 x Mo17 and B84 x Mo17 were 7.50 and 8.39 Mg ha^{-1}, respectively.

Analysis of variance for the S_0 experiments (Table A1, Appendix) indicated that entry and entry x environment interaction mean squares were significant for all traits. The combined analysis of variance for S_1 experiments over 1988 and 1989, and over 1989 are presented in Tables A2 and A3, respectively. The entry mean squares from these analyses of variance were significant for all traits except root lodging. Entry x environment interaction mean square for the combined analysis of variance of the S_1 experiments over 1988 and 1989 was significant for grain yield, root lodging, stalk lodging, silking date, pollen date ($p < 0.01$), and plant height ($p < 0.05$). Significant differences were not detected for grain moisture and ear height. For the combined analysis of variance of the S_1 experiments over 1989, the entry x environment interaction mean square was significant for root lodging, stalk lodging ($p < 0.01$), and grain moisture ($p < 0.05$).

Mean squares for the partitions of population, population crosses and testcrosses into linear, quadratic, and lack of fit are included in the combined analyses of variance (Tables A1 to A3). When lack of fit

was significant, the cubic term was tested for significance. In most instances, the cubic models were not significant.

Percentage of direct and indirect response per cycle of selection were estimated using the intercept and linear coefficient from the linear regression model (Table 1). Means over environments and regression coefficients for populations and crosses of S_0 and S_1 generations for each trait are presented in Tables 2 to 9. For grain yield, rate of response for the interpopulation cross (direct response) was greater than the populations per se (indirect response) for both S_0 and S_1 generations. The direct response was 6.95% cycle^{-1} (b_ℓ = 0.28 $\pm$ 0.02 Mg ha^{-1} cycle^{-1}) for the S_0 generation and 4.96% cycle^{-1} (b_ℓ = 0.18 $\pm$ 0.02 Mg ha^{-1} cycle^{-1}) for the S_1 generation. For S_0 generation, BSCB1(R)Cn showed greater rate of response to selection than BSSS(R)Cn (1.94 vs 1.66% cycle^{-1}), but the response in BSSS(R)Cn was not significant. The indirect response observed in S_1 generation was greater in BSSS(R)Cn than in BSCB1(R)Cn and the response in BSCB1(R)Cn was not significant. The indirect response was 0.77% cycle^{-1} for S_1 generation of BSCB1(R)Cn and 3.25% cycle^{-1} for S_1 generation of BSSS(R)Cn.

Quadratic effects for grain yield were significant only for the BSSS(R)Cn x Mo17 testcrosses and the S_1 generation of the BSSS(R)Cn x BSCB1(R)Cn interpopulation crosses (Table 2). However, the quadratic sum of squares in both instances were at least seven times smaller than the linear sum of squares (Tables A1 and A3). Except for the S_0 generation of BSSS(R)Cn and the S_1 generation of BSCB1(R)Cn, the linear regression coefficients were significant in all other instances. The S_0 generation

Table 1. Direct and indirect responses per cycle of selection expressed by the linear coefficient as a percentage of the intercept for eight traits

Traits	Populations and crosses		
	BSSS(R)	BSSS(R) x BSCB1(R)	BSCB1(R)
	----------S_0----------		
Grain yield	1.66	6.95	1.94
Grain moisture	0.00	0.32	0.11
Root lodging	-5.65	-2.32	-5.58
Stalk lodging	-2.83	-5.12	-7.57
Ear height	-0.71	0.33	-0.78
Plant height	-0.02	0.78	-0.13
Silking date	-0.39	-0.28	0.14
Pollen date	-0.17	-0.02	0.34
	----------S_1----------		
Grain yield	3.25	4.96	0.77
Grain moisture	0.19	0.77	0.39
Root lodging	-4.50	-4.01	-2.87
Stalk lodging	-4.18	-6.21	-8.45
Ear height	-0.24	0.64	-0.85
Plant height	0.53	0.98	-0.37
Silking date	-0.27	-0.06	0.09
Pollen date	-0.16	0.21	0.19

Table 2. Means over seven environments and least square estimates of response to reciprocal recurrent selection for grain yield of BSSS(R) and BSCB1(R) populations and crosses

Entry	Mean of check	Cycle of selection C0	C4	C7	C8	C9
S_0 population						
Per se and crosses						
BSSS(R)		3.55[c]	3.76	4.24	4.34	4.25
BSCB1(R)		3.21[c]	3.16	3.61	3.30	3.87
BSSS(R) x BSCB1(R)		4.24[c]	4.94[c]	6.08[c]	6.59	6.94[c]
Testcrosses						
BSSS(R) x BSSS(R)C0		3.55[c]	4.00	4.54	--[d]	4.92
BSSS(R) x BSCB1(R)C0		4.24[c]	4.16	5.10	--	5.20
BSCB1(R) x BSCB1(R)C0		3.21[c]	3.48	4.14	--	4.92
BSCB1(R) x BSSS(R)C0		4.24[c]	4.37	4.96	--	5.50
BSSS(R) x B73		5.63	5.80	6.98	6.53	6.96
BSSS(R) x Mo17		5.61	6.25	7.00	7.20	7.57
BSCB1(R) x B73		6.19	6.37	7.05	7.33	7.40
BSCB1(R) x Mo17		4.99	5.27	5.96	6.07	6.44
Check						
B73 x Mo17	7.50					
B84 x Mo17	8.47					
B89 x Mo17	7.49					
S_1 population						
BSSS(R)		2.40	2.88	2.83	3.34	3.39
BSCB1(R)		2.55	2.83	2.52	2.62	2.74
BSSS(R) x BSCB1(R)[e]		3.41	4.40	5.13	5.39	5.38

[a] b_0 is an estimate of C0 mean; b_ℓ is an estimate of the average rate of response per cycle; b_q is included to indicate when the quadratic term accounted for a significant proportion of deviation sums of squares.

[b] Standard error of mean of duplicate entries is $SE/\sqrt{2}$.

[c] Mean of duplicate entries.

[d] No data were obtained.

[e] Means over three environments.

*,**Significant at the 0.05 and 0.01 probability levels, respectively.

C10	C11	SE[b]	Regression coefficients[a] b_0	b_ℓ	b_q
3.98	3.92	0.24	3.61	0.06 ± 0.02	--
3.59	3.76		3.09	0.06 ± 0.02*	--
6.84	6.76[c]		4.03	0.28 ± 0.02**	--
--	4.84		3.61	0.13 ± 0.02*	--
--	5.51		4.03	0.13 ± 0.02**	--
--	4.81		3.09	0.17 ± 0.02**	--
--	5.86		4.03	0.15 ± 0.02**	--
6.31	6.71		5.67	0.11 ± 0.03**	--
6.99	6.92		5.76	0.15 ± 0.03**	*
7.59	7.91		6.00	0.16 ± 0.03**	--
6.67	6.99		4.77	0.18 ± 0.03**	--
3.22	3.28	0.17	2.46	0.08 ± 0.02**	--
2.92	2.80		2.57	0.02 ± 0.02	--
5.47	5.09	0.21	3.63	0.18 ± 0.02**	**

Table 3. Means over seven environments and least square estimates of response to reciprocal recurrent selection for grain moisture of BSSS(R) and BSCB1(R) populations and crosses

Entry	Mean of check	Cycle of selection C0	C4	C7	C8	C9
S_0 population						
Per se and crosses						
BSSS(R)		21.4[c]	19.4	21.0	21.2	21.0
BSCB1(R)		17.5[c]	17.1	17.9	19.2	17.6
BSSS(R) x BSCB1(R)		19.0[c]	18.4[c]	19.7[c]	20.1	19.3[c]
Testcrosses						
BSSS(R) x BSSS(R)C0		21.4[c]	20.7	21.4	--[d]	20.9
BSSS(R) x BSCB1(R)C0		19.0[c]	17.6	18.7	--	18.6
BSCB1(R) x BSCB1(R)C0		17.5[c]	17.9	17.7	--	17.6
BSCB1(R) x BSSS(R)C0		19.0[c]	19.2	19.4	--	18.8
BSSS(R) x B73		21.0	19.6	20.7	21.1	21.0
BSSS(R) x Mo17		19.9	19.7	20.5	21.3	21.3
BSCB1(R) x B73		19.3	19.1	19.3	19.5	19.1
BSCB1(R) x Mo17		18.7	18.2	18.4	18.8	18.4
Check						
B73 x Mo17	19.6					
B84 x Mo17	20.3					
B89 x Mo17	19.6					
S_1 population						
BSSS(R)		21.5	20.2	22.0	22.3	21.5
BSCB1(R)		18.0	18.1	18.7	19.3	18.7
BSSS(R) x BSCB1(R)[e]		19.3	20.5	20.2	20.8	20.9

[a]b_0 is an estimate of C0 mean; b_ℓ is an estimate of the average rate of response per cycle; b_q is included to indicate when the quadratic term accounted for a significant proportion of deviation sums of squares.

[b]Standard error of mean of duplicate entries is $SE/\sqrt{2}$.

[c]Mean of duplicate entries.

[d]No data were obtained.

[e]Means over three environments.

*,**Significant at the 0.05 and 0.01 probability levels, respectively.

C10	C11	SE[b]	Regression coefficients[a] b_0	b_ℓ	b_q
20.3	21.7	0.38	20.88	0.00 ± 0.03	--
17.3	17.6		17.59	0.02 ± 0.03	--
19.3	18.9[c]		18.75	0.06 ± 0.03*	--
--	21.4		20.88	0.03 ± 0.03**	--
--	19.2		18.75	-0.00 ± 0.03	--
--	17.5		17.59	0.00 ± 0.03	*
--	18.9		18.75	0.03 ± 0.03	--
20.4	21.1		20.47	0.03 ± 0.04	--
20.3	21.0		19.74	0.12 ± 0.04**	--
19.6	19.7		19.14	0.03 ± 0.04	--
17.7	17.8		18.73	-0.06 ± 0.04	--
21.5	21.1	0.35	21.20	0.04 ± 0.04	--
18.2	18.7		18.07	0.07 ± 0.04	--
20.7	21.3	0.51	19.47	0.15 ± 0.05**	--

Table 4. Means over seven environments and least square estimates of response to reciprocal recurrent selection for root lodging of BSSS(R) and BSCB1(R) populations and crosses

Entry	Mean of check	Cycle of selection C0	C4	C7	C8	C9
S_0 population						
Per se and crosses						
BSSS(R)		6.8[c]	2.7	4.7	5.9	3.9
BSCB1(R)		14.0[c]	8.0	5.5	8.1	6.9
BSSS(R) x BSCB1(R)		9.1[c]	8.9[c]	6.4[c]	10.1	10.0[c]
Testcrosses						
BSSS(R) x BSSS(R)C0		6.8[c]	5.6	7.7	--[d]	3.4
BSSS(R) x BSCB1(R)C0		9.1[c]	8.2	8.2	--	5.9
BSCB1(R) x BSCB1(R)C0		14.0[c]	10.3	9.5	--	11.0
BSCB1(R) x BSSS(R)C0		9.1[c]	9.3	6.7	--	3.9
BSSS(R) x B73		4.4	3.6	4.5	8.6	5.9
BSSS(R) x Mo17		6.3	3.5	4.5	6.0	4.7
BSCB1(R) x B73		8.9	7.3	12.1	10.4	8.5
BSCB1(R) x Mo17		6.5	10.1	5.4	7.1	7.2
Check						
B73 x Mo17	4.0					
B84 x Mo17	10.7					
B89 x Mo17	2.0					
S_1 population						
BSSS(R)		4.8	2.8	4.6	4.8	3.0
BSCB1(R)		10.0	7.6	5.4	4.9	5.6
BSSS(R) x BSCB1(R)[e]		13.6	9.2	7.0	8.1	7.8

[a]b_0 is an estimate of C0 mean; b_ℓ is an estimate of the average rate of response per cycle; b_q is included to indicate when the quadratic term accounted for a significant proportion of deviation sums of squares.

[b]Standard error of mean of duplicate entries is $SE/\sqrt{2}$.

[c]Mean of duplicate entries.

[d]No data were obtained.

[e]Means over three environments.

*,**Significant at the 0.05 and 0.01 probability levels, respectively.

C10	C11	SE[b]	Regression coefficients[a]		
			b_0	b_ℓ	b_q
3.4	0.2	2.39	6.55	-0.37 ± 0.20*	--
6.4	5.6		12.91	-0.72 ± 0.20*	--
6.0	5.7[c]		9.49	-0.22 ± 0.17	--
--	6.2		6.55	-0.10 ± 0.22	--
--	7.3		9.49	-0.27 ± 0.21	--
--	7.4		12.91	-0.42 ± 0.22	--
--	7.0		9.49	-0.37 ± 0.21	--
2.9	2.8		4.78	-0.01 ± 0.26	--
5.2	4.8		5.35	-0.05 ± 0.26	--
8.8	9.2		8.81	0.07 ± 0.26	--
4.7	6.6		7.90	-0.16 ± 0.26	--
2.1	1.4	2.02	4.89	-0.22 ± 0.22	--
6.5	8.8		8.72	-0.25 ± 0.22	--
7.4	8.5	3.79	12.21	-0.49 ± 0.40	--

Table 5. Means over seven environments and least square estimates of response to reciprocal recurrent selection for stalk lodging of BSSS(R) and BSCB1(R) populations and crosses

Entry	Mean of check	Cycle of selection C0	C4	C7	C8	C9
S_0 population						
Per se and crosses						
BSSS(R)		19.8[c]	21.4	17.3	13.8	16.0
BSCB1(R)		40.4[c]	32.4	18.3	12.2	10.5
BSSS(R) x BSCB1(R)		25.0[c]	30.4[c]	19.8[c]	13.9	14.9[c]
Testcrosses						
BSSS(R) x BSSS(R)C0		19.8[c]	17.9	17.1	--[d]	17.9
BSSS(R) x BSCB1(R)C0		25.0[c]	29.0	24.9	--	25.3
BSCB1(R) x BSCB1(R)C0		40.4[c]	37.5	31.9	--	25.4
BSCB1(R) x BSSS(R)C0		25.0[c]	26.7	20.7	--	17.4
BSSS(R) x B73		16.3	17.7	13.7	16.5	12.9
BSSS(R) x Mo17		12.3	13.1	11.2	8.3	9.9
BSCB1(R) x B73		19.6	17.5	12.2	11.2	8.5
BSCB1(R) x Mo17		16.5	22.0	13.3	14.1	14.4
Check						
B73 x Mo17	8.2					
B84 x Mo17	8.6					
B89 x Mo17	4.2					
S_1 population						
BSSS(R)		11.3	9.9	7.5	3.8	7.5
BSCB1(R)		25.0	17.1	7.7	4.9	5.1
BSSS(R) x BSCB1(R)[e]		14.1	14.7	4.3	8.1	4.3

[a] b_0 is an estimate of C0 mean; b_ℓ is an estimate of the average rate of response per cycle; b_q is included to indicate when the quadratic term accounted for a significant proportion of deviation sums of squares.

[b] Standard error of mean of duplicate entries is $SE/\sqrt{2}$.

[c] Mean of duplicate entries.

[d] No data were obtained.

[e] Means over three environments.

*,**Significant at the 0.05 and 0.01 probability levels, respectively.

C10	C11	SE[b]	Regression coefficients[a] b_0	b_ℓ	b_q
17.6	10.9	2.23	20.52	-0.58 ± 0.18*	--
11.8	9.7		41.23	-3.12 ± 0.18**	--
16.2	11.4[c]		29.66	-1.52 ± 0.16**	**
--	16.1		20.52	-0.40 ± 0.21	--
--	24.2		29.66	-0.51 ± 0.19**	--
--	26.2		41.23	-1.45 ± 0.21**	--
--	16.8		29.66	-1.22 ± 0.19**	--
16.8	12.8		17.10	-0.26 ± 0.24	--
10.9	9.4		12.88	-0.31 ± 0.24	--
9.9	11.4		19.76	-0.98 ± 0.24**	--
12.2	15.1		18.68	-0.47 ± 0.24*	--
8.1	6.2	1.72	11.01	-0.46 ± 0.25*	--
6.8	2.5		24.25	-2.05 ± 0.18**	--
7.7	5.6	2.78	14.81	-0.92 ± 0.30**	--

Table 6. Means over seven environments and least square estimates of response to reciprocal recurrent selection for ear height of BSSS(R) and BSCB1(R) populations and crosses

Entry	Mean of check	Cycle of selection C0	C4	C7	C8
S_0 population					
Per se and crosses					
BSSS(R)		114.9[c]	104.1	106.1	104.5
BSCB1(R)		103.7[c]	100.6	102.0	102.5
BSSS(R) x BSCB1(R)		113.3[c]	113.6[c]	114.7[c]	117.7
Testcrosses					
BSSS(R) x BSSS(R)C0		114.9[c]	108.6	110.3	--[d]
BSSS(R) x BSCB1(R)C0		113.3[c]	110.2	112.4	--
BSCB1(R) x BSCB1(R)C0		103.7[c]	107.4	108.7	--
BSCB1(R) x BSSS(R)C0		113.3[c]	116.4	118.4	--
BSSS(R) x B73		118.4	113.1	115.1	118.0
BSSS(R) x Mo17		116.7	112.4	114.9	115.6
BSCB1(R) x B73		116.2	120.6	119.0	119.5
BSCB1(R) x Mo17		108.3	111.8	112.8	116.3
Check					
B73 x Mo17	117.6				
B84 x Mo17	117.5				
B89 x Mo17	104.4				
S_1 population					
BSSS(R)		89.2	85.7	87.8	86.7
BSCB1(R)		82.6	82.3	80.7	80.7
BSSS(R) x BSCB1(R)[e]		95.2	97.9	97.0	99.9

[a] b_0 is an estimate of C0 mean; b_ℓ is an estimate of the average rate of response per cycle; b_q is included to indicate when the quadratic term accounted for a significant proportion of deviation sums of squares.

[b] Standard error of mean of duplicate entries is $SE/\sqrt{2}$.

[c] Mean of duplicate entries.

[d] No data were obtained.

[e] Means over three environments.

*,**Significant at the 0.05 and 0.01 probability levels, respectively.

				Regression coefficients[a]		
C9	C10	C11	SE[b]	b_0	b_ℓ	b_q
107.2	105.7	103.0	1.88	112.11	-0.80 ± 0.16**	--
95.3	96.4	94.3		105.04	-0.82 ± 0.16**	--
117.7[c]	118.4	115.5[c]		113.00	0.37 ± 0.13**	--
113.6	--	113.1		112.11	-0.01 ± 0.17	*
113.0	--	113.4		113.00	-0.04 ± 0.16	--
107.2	--	105.0		105.04	0.20 ± 0.17	*
113.4	--	116.7		113.00	0.36 ± 0.16**	--
121.9	116.2	115.3		116.58	0.04 ± 0.20	--
117.6	117.2	115.6		114.86	0.12 ± 0.20	--
118.6	117.5	119.8		117.69	0.15 ± 0.20	--
114.8	112.4	111.0		109.81	0.38 ± 0.20	--
86.2	86.3	86.3	1.81	88.34	-0.21 ± 0.19	--
77.6	76.1	74.3		84.25	-0.72 ± 0.19**	*
99.3	104.9	100.1	2.36	94.93	0.61 ± 0.25*	--

Table 7. Means over seven environments and least square estimates of response to reciprocal recurrent selection for plant height of BSSS(R) and BSCB1(R) populations and crosses

Entry	Mean of check	Cycle of selection C0	C4	C7	C8
S_0 population					
Per se and crosses					
BSSS(R)		218.0[c]	207.6	212.1	219.0
BSCB1(R)		204.0[c]	201.2	208.3	207.7
BSSS(R) x BSCB1(R)		215.5[c]	219.8[c]	225.6[c]	231.5
Testcrosses					
BSSS(R) x BSSS(R)C0		218.0[c]	213.3	213.1	--[d]
BSSS(R) x BSCB1(R)C0		215.5[c]	217.1	221.5	--
BSCB1(R) x BSCB1(R)C0		204.0[c]	214.5	215.4	--
BSCB1(R) x BSSS(R)C0		215.5[c]	220.9	227.8	--
BSSS(R) x B73		225.8	216.9	224.5	226.7
BSSS(R) x Mo17		219.2	219.1	220.8	226.8
BSCB1(R) x B73		116.2	120.6	119.0	119.5
BSCB1(R) x Mo17		108.3	111.8	112.8	116.3
Check					
B73 x Mo17	224.9				
B84 x Mo17	224.6				
B89 x Mo17	216.2				
S_1 population					
BSSS(R)		180.1	175.1	180.5	192.7
BSCB1(R)		173.9	174.4	174.8	176.6
BSSS(R) x BSCB1(R)[e]		194.8	199.0	204.3	211.1

[a]b_0 is an estimate of C0 mean; b_ℓ is an estimate of the average rate of response per cycle; b_q is included to indicate when the quadratic term accounted for a significant proportion of deviation sums of squares.

[b]Standard error of mean of duplicate entries is $SE/\sqrt{2}$.

[c]Mean of duplicate entries.

[d]No data were obtained.

[e]Means over three environments.

*,**Significant at the 0.05 and 0.01 probability levels, respectively.

C9	C10	C11	SE[b]	Regression coefficients[a] b_0	b_ℓ	b_q
217.0	217.0	210.0	2.46	214.73	-0.05 ± 0.20	--
203.0	202.7	199.7		205.96	-0.27 ± 0.20**	--
234.1[c]	236.7	229.9[c]		215.30	1.69 ± 0.17**	--
221.8	--	221.7		214.73	0.46 ± 0.22*	*
225.9	--	224.1		215.30	0.91 ± 0.21**	--
216.4	--	216.3		205.96	1.15 ± 0.22**	*
219.7	--	226.5		215.30	1.02 ± 0.21**	--
230.4	219.6	221.4		223.57	0.01 ± 0.26	--
227.2	225.9	222.1		218.59	0.63 ± 0.26*	--
118.6	117.5	119.8		225.97	0.79 ± 0.26**	--
114.8	112.4	111.0		213.20	0.52 ± 0.26*	--
187.8	185.8	185.7	2.45	177.39	0.94 ± 0.26**	--
169.1	168.3	165.9		176.41	-0.65 ± 0.26*	*
206.7	220.7	210.4	2.18	193.38	1.90 ± 0.30**	--

Table 8. Means over seven environments and least square estimates of response to reciprocal recurrent selection for silking date of BSSS(R) and BSCB1(R) populations and crosses

Entry	Mean of check	Cycle of selection C0	C4	C7	C8	C9
S_0 population						
Per se and crosses						
BSSS(R)		89.3[c]	86.4	86.5	86.4	85.3
BSCB1(R)		83.4[c]	86.7	86.1	86.4	84.9
BSSS(R) x BSCB1(R)		86.0[c]	84.8[c]	84.8[c]	84.9	83.6[c]
Testcrosses						
BSSS(R) x BSSS(R)C0		89.3[c]	83.7	83.9	--[d]	82.9
BSSS(R) x BSCB1(R)C0		86.0[c]	84.3	82.5	--	82.7
BSCB1(R) x BSCB1(R)C0		83.4[c]	84.6	84.1	--	83.6
BSCB1(R) x BSSS(R)C0		86.0[c]	86.2	86.8	--	85.3
BSSS(R) x B73		87.2	85.2	84.0	84.1	83.9
BSSS(R) x Mo17		86.4	84.6	83.8	84.4	84.0
BSCB1(R) x B73		83.6	84.4	84.7	83.9	84.4
BSCB1(R) x Mo17		84.3	84.4	84.6	84.6	83.8
Check						
B73 x Mo17	84.0					
B84 x Mo17	83.1					
B89 x Mo17	83.7					
S_1 population						
BSSS(R)		89.7	88.7	89.2	88.2	87.3
BSCB1(R)		86.0	87.8	88.2	88.2	87.0
BSSS(R) x BSCB1(R)[e]		90.0	90.3	90.0	90.3	89.3

[a] b_0 is an estimate of C0 mean; b_ℓ is an estimate of the average rate of response per cycle; b_q is included to indicate when the quadratic term accounted for a significant proportion of deviation sums of squares.

[b] Standard error of mean of duplicate entries is $SE/\sqrt{2}$.

[c] Mean of duplicate entries.

[d] No data were obtained.

[e] Means over three environments.

*,**Significant at the 0.05 and 0.01 probability levels, respectively.

C10	C11	SE[b]	Regression coefficients[a] b_0	b_ℓ	b_q
85.3	85.3	0.55	88.86	-0.35 ± 0.04**	--
84.8	84.9		84.36	0.12 ± 0.05**	**
83.3	83.2[c]		86.02	-0.24 ± 0.04**	--
--	83.9		88.86	-0.24 ± 0.05**	--
--	82.5		86.02	-0.37 ± 0.05**	--
--	83.6		84.36	-0.06 ± 0.05	--
--	85.7		86.02	-0.01 ± 0.05**	--
83.7	84.0		86.73	-0.31 ± 0.06**	--
83.9	83.4		86.02	-0.24 ± 0.06**	--
83.8	84.2		83.94	0.03 ± 0.06	--
83.4	83.5		84.63	-0.08 ± 0.06	--
87.0	87.3	0.69	89.87	-0.24 ± 0.08**	--
86.7	87.5		86.79	0.08 ± 0.07	*
89.7	89.7	0.42	90.23	-0.05 ± 0.05	--

Table 9. Means over seven environments and least square estimates of response to reciprocal recurrent selection for pollen date of BSSS(R) and BSCB1(R) populations and crosses

Entry	Mean of check	Cycle of selection C0	C4	C7	C8	C9
S_0 population						
Per se and crosses						
BSSS(R)		85.5[c]	82.7	83.2	84.1	83.4
BSCB1(R)		79.2[c]	82.4	82.9	83.5	82.1
BSSS(R) x BSCB1(R)		81.8[c]	80.9[c]	81.7[c]	82.1	81.5[c]
Testcrosses						
BSSS(R) x BSSS(R)C0		85.5[c]	83.7	83.9	--[d]	82.9
BSSS(R) x BSCB1(R)C0		81.8[c]	84.3	82.5	--	82.7
BSCB1(R) x BSCB1(R)C0		79.2[c]	80.7	80.4	--	81.2
BSCB1(R) x BSSS(R)C0		81.8[c]	82.4	82.9	--	81.7
BSSS(R) x B73		83.9	82.9	82.8	82.2	82.6
BSSS(R) x Mo17		81.7	81.3	81.0	81.0	81.2
BSCB1(R) x B73		80.3	81.7	81.9	81.9	81.9
BSCB1(R) x Mo17		80.4	80.8	81.0	81.3	81.1
Check						
B73 x Mo17	81.0					
B84 x Mo17	80.6					
B89 x Mo17	80.5					
S_1 population						
BSSS(R)		86.5	85.5	85.7	85.0	84.7
BSCB1(R)		81.8	83.8	84.7	84.5	83.8
BSSS(R) x BSCB1(R)[e]		84.3	85.3	85.3	86.3	85.0

[a]b_0 is an estimate of C0 mean; b_ℓ is an estimate of the average rate of response per cycle; b_q is included to indicate when the quadratic term accounted for a significant proportion of deviation sums of squares.

[b]Standard error of mean of duplicate entries is $SE/\sqrt{2}$.

[c]Mean of duplicate entries.

[d]No data were obtained.

[e]Means over three environments.

*,**Significant at the 0.05 and 0.01 probability levels, respectively.

C10	C11	SE[b]	Regression coefficients[a] b_0	b_ℓ	b_q
83.3	83.9	0.44	84.77	-0.14 ± 0.04*	**
81.4	82.5		80.06	0.27 ± 0.04**	**
81.3	81.2[c]		81.56	-0.02 ± 0.03	--
--	83.9		84.77	-0.14 ± 0.04**	*
--	82.5		81.56	-0.17 ± 0.04**	--
--	79.9		80.06	0.05 ± 0.04	**
--	82.5		81.56	0.09 ± 0.04**	--
82.4	82.2		83.72	-0.14 ± 0.05**	--
81.2	81.6		81.48	-0.03 ± 0.05	--
81.4	81.8		80.77	0.11 ± 0.05*	--
80.9	80.1		80.69	0.02 ± 0.05	--
84.7	85.3	0.71	86.32	-0.14 ± 0.08	--
83.2	84.2		82.56	0.16 ± 0.08*	*
86.3	86.7	0.61	84.33	0.18 ± 0.06**	--

of BSCB1(R)Cn and BSSS(R)Cn x BSCB1(R)Cn showed significant grain yield improvement at the rate of 0.06 ± 0.02 and 0.28 ± 0.02 Mg ha^{-1} $cycle^{-1}$, respectively. Grain yield did not change significantly for the S_0 generation of BSSS(R)Cn (0.06 ± 0.02 Mg ha^{-1} $cycle^{-1}$), but a significant change was detected in the S_1 generation (0.08 ± 0.02 Mg ha^{-1} $cycle^{-1}$). The S_1 generation of BSCB1(R)Cn did not change significantly with selection (0.02 ± 0.02 Mg ha^{-1} $cycle^{-1}$). Mean grain yield of the S_0 generation of BSSS(R)C11 x BSCB1(R)C11 was about 80 and 90% of mean grain yields of single-cross checks, B84 x Mo17 and B73 x Mo17, respectively.

The linear regression coefficients of the testcrosses of the populations with the C0 population and the C0 of the reciprocal population were significant in all instances but the rates of response were approximately half of that observed in S_0 generation of BSSS(R)Cn x BSCB1(R)Cn. Testcrosses of BSCB1(R)Cn to the C0 populations showed greater rates of response than testcrosses of BSSS(R)Cn to the C0 populations, although the differences were not significant. Of the BSSS(R)Cn testcrosses, BSSS(R)Cn x BSSS(R)C0 and BSSS(R)Cn x BSCB1(R)C0 showed significant increases in grain yield at the same rate of 0.13 ± 0.02 Mg ha^{-1} $cycle^{-1}$. The rates of improvement were significant for BSCB1(R)Cn x BSCB1(R)C0 (0.17 ± 0.02 Mg ha^{-1} $cycle^{-1}$) and for BSCB1(R)Cn x BSSS(R)C0 (0.15 ± 0.02 Mg ha^{-1} $cycle^{-1}$).

Significant increases in grain yield were observed in the testcrosses of BSSS(R)Cn and BSCB1(R)Cn to the inbred testers B73 and Mo17. The quadratic response in BSSS(R)Cn x Mo17 may have been caused by the rapid increase in grain yield from C0 to C9 followed by a slight

decrease from C9 to C11. The linear regression coefficient from the linear model for BSSS(R)Cn x Mo17 was significant at 0.15 ± 0.03 Mg ha^{-1} $cycle^{-1}$. The response of BSSS(R)Cn x B73 was significant at 0.11 ± 0.03 Mg ha^{-1} $cycle^{-1}$. Increases in grain yield of BSCB1(R)Cn x B73 and BSCB1(R)Cn x Mo17 were significant at the rate of 0.16 ± 0.03 and 0.18 ± 0.03 Mg ha^{-1} $cycle^{-1}$, respectively. As in the testcrosses of populations with C0 populations, testcrosses of BSCB1(R)Cn with inbred testers tended to show greater rates of response than testcrosses of BSSS(R)Cn with inbred testers, although the differences were not significant. The greatest mean grain yield of the populations testcrossed to the inbreds was observed for BSCB1(R)C11 x B73 (7.91 Mg ha^{-1}), which was greater than the single-cross check, B73 x Mo17 (7.50 Mg ha^{-1}) but less than B84 x Mo17 (8.47 Mg ha^{-1}).

Significant midparent heterosis for grain yield was observed for all interpopulation crosses (Table 10). The heterosis increased consistently from 0.86 Mg ha^{-1} for the cross of C0 x C0 to 2.92 Mg ha^{-1} for the cross of C11 x C11. Mid-parent heterosis for grain yield expressed as the percentage of the midparent increased from 25.44% to 76.04% after 11 cycles of selection (Table 11).

Significant inbreeding depression for grain yield was detected for all populations and population crosses except BSCB1(R)C4 (Table 12). The inbreeding depression for BSSS(R)Cn decreased from 1.15 Mg ha^{-1} in C0 to 0.64 Mg ha^{-1} in C11 but a trend was not apparent in BSCB1(R)Cn. Inbreeding depression in the population crosses steadily increased from 1.01 Mg ha^{-1} to 2.32 Mg ha^{-1}.

Table 10. Actual units of midparent heterosis in the population crosses of BSSS(R) and BSCB1(R) for the eight traits

Population crosses	Traits							
	Grain		Lodging		Height		Date	
	Yield	Moisture	Root	Stalk	Ear	Plant	Silking	Pollen
	Mg ha^{-1}	----------%	----------		-------cm-------		------days------	
BSSS(R)C0 x BSCB1(R)C0	0.86**	-0.45	-1.30	-5.10**	3.90*	4.30*	-0.35	-0.55
BSSS(R)C4 x BSCB1(R)C4	1.48**	0.15	3.55	3.50	11.25**	15.40**	-1.75**	-1.65**
BSSS(R)C7 x BSCB1(R)C7	2.16**	0.25	1.30	2.00	10.65**	15.40**	-1.60**	-1.30**
BSSS(R)C8 x BSCB1(R)C8	2.77**	-0.10	3.10	0.90	14.20**	18.15**	-1.55*	-1.80**
BSSS(R)C9 x BSCB1(R)C9	2.88**	0.00	4.40	1.65	16.45**	24.10**	-1.50**	-1.20**
BSSS(R)C10 x BSCB1(R)C10	3.06**	0.50	1.10	1.50	17.35**	26.85**	-1.80**	-1.15*
BSSS(R)C11 x BSCB1(R)C11	2.92**	-0.75*	2.80	1.10	16.85**	25.05**	-1.85**	-1.95**

*,**Significant at the 0.05 and 0.01 probability levels, respectively.

Table 11. Percentage of midparent heterosis in the population crosses of BSSS(R) and BSCB1(R) for the eight traits

Population crosses	Traits							
	Grain		Lodging		Height		Date	
	Grain	Moisture	Root	Stalk	Ear	Plant	Silking	Pollen
BSSS(R)C0 x BSCB1(R)C0	25.44	-2.31	-12.50	-16.94	3.57	2.04	-0.41	-0.67
BSSS(R)C4 x BSCB1(R)C4	42.77	0.82	66.36	13.01	10.99	7.53	-2.02	-2.00
BSSS(R)C7 x BSCB1(R)C7	54.90	1.29	25.49	11.24	10.24	7.33	-1.85	-1.57
BSSS(R)C8 x BSCB1(R)C8	72.51	-0.50	44.29	6.92	13.72	8.51	-1.80	-2.15
BSSS(R)C9 x BSCB1(R)C9	70.94	0.00	81.48	12.45	16.25	11.48	-1.76	-1.45
BSSS(R)C10 x BSCB1(R)C10	80.47	2.66	22.45	10.20	17.17	12.79	-2.12	-1.40
BSSS(R)C11 x BSCB1(R)C11	76.04	-3.82	96.55	10.68	17.08	12.23	-2.18	-2.35

Table 12. Inbreeding depression in actual units for the BSSS(R) and BSCB1(R) populations and their crosses for eight traits over environments

Populations and crosses	Grain		Lodging	
	Yield	Moisture	Root	Stalk
	Mg ha^{-1}	----------%	----------	
BSSS(R)C0	1.15**	-0.1	2.0	8.5**
BSSS(R)C4	0.88**	-0.8	-0.1	11.5**
BSSS(R)C7	1.41**	-1.0	0.1	9.8**
BSSS(R)C8	1.00**	-1.1*	1.1	10.0**
BSSS(R)C9	0.86**	-0.5	0.9	8.5**
BSSS(R)C10	0.76*	-1.2*	1.3	9.5**
BSSS(R)C11	0.64*	0.6	-1.2	4.7
BSCB1(R)C0	0.66*	-0.5	4.0	15.4**
BSCB1(R)C4	0.33	-1.0	0.4	15.3**
BSCB1(R)C7	1.09**	-0.8	0.1	10.6**
BSCB1(R)C8	0.68*	-0.1	3.2	7.3**
BSCB1(R)C9	1.13**	-1.1*	1.3	5.4
BSCB1(R)C10	0.67*	-0.9	-0.1	5.0
BSCB1(R)C11	0.96**	-1.1*	-3.2	7.2**
BSSS(R)C0 x BSCB1(R)C0[a]	1.01**	0.0	3.5	16.4**
BSSS(R)C4 x BSCB1(R)C4	0.92**	-1.9**	7.0	14.6**
BSSS(R)C7 x BSCB1(R)C7	1.62**	0.0	4.2	14.4**
BSSS(R)C8 x BSCB1(R)C8	2.11**	-0.5	9.9	9.8*
BSSS(R)C9 x BSCB1(R)C9	2.31**	-0.7	11.6*	10.4**
BSSS(R)C10 x BSCB1(R)C10	2.31**	-1.3	4.1	9.9*
BSSS(R)C11 x BSCB1(R)C11	2.32**	-2.0**	2.7	7.8*

[a]Traits were evaluated in three environments, silking and pollen date were evaluated in only one environment.

*,**Difference between S_0 and S_1 generations significant at 0.05 and 0.01 probability levels, respectively.

Height		Date	
Ear	Plant	Silking	Pollen
----------cm----------		----------days----------	
25.7**	37.9**	-0.4	-1.0
18.4**	32.5**	-2.3*	-2.8**
18.3**	31.5**	-2.7**	-2.5**
17.8**	26.3**	-1.8*	-0.9
21.0**	29.2**	-2.0*	-1.4
19.4**	31.2**	-1.8*	-1.4
16.7**	24.3**	-2.0*	-1.5
21.1**	30.5**	-2.6**	-2.6**
18.3**	26.8**	-1.1	-1.4
21.3**	33.5**	-2.1*	-1.9*
21.8**	31.1**	-1.9*	-1.0
17.7**	30.9**	-2.1*	-1.7
20.3**	34.4**	-1.9*	-1.8*
20.0**	33.8**	-2.7**	-1.7
27.3**	35.5**	-1.0	-0.5
22.1**	30.5**	-2.0**	-1.5*
25.1**	33.6**	-2.4**	-1.5*
23.6**	30.6**	-3.0**	-2.6**
24.1**	37.7**	-3.1**	-1.0
18.6**	26.8**	-3.4**	-2.2**
21.7**	31.1**	-4.1**	-3.0**

Grain moisture remained unchanged for BSSS(R)Cn and BSCB1(R)Cn populations per se, and increased slightly for interpopulation crosses for the S_0 and S_1 generations (Table 3). Little or no change in grain moisture was also observed for the testcrosses of the populations to the CO populations and inbred testers. Percentage root lodging decreased for the S_0 and S_1 generations of all populations and testcrosses of the population to the CO populations and inbred testers (Table 4). However, the linear decrease in percentage root lodging was significant only for the S_0 generation of BSSS(R) ($-0.37 \pm 0.20\%$ cycle^{-1}) and BSCB1(R) ($-0.72 \pm 0.20\%$ cycle^{-1}). The S_0 generation of BSSS(R)C11 had 0.2% root lodging which was lower than the three single-cross checks.

A reduction in percentage of stalk lodging was observed for the S_0 and S_1 generations of all populations per se and testcrosses of the populations to the CO populations and inbred testers (Table 5). The linear response per cycle was significant in all instances, except BSSS(R)Cn x BSSS(R)CO and testcrosses of BSSS(R)Cn to B73 and Mo17. A quadratic trend was observed in S_0 generation of BSSS(R)Cn x BSCB1(R)Cn. For both S_0 and S_1 generations, the rate of direct response for stalk lodging expressed as a percentage of the intercept was intermediate to that of indirect response (Table 1). The direct response for the S_0 generation was -5.12% cycle^{-1} ($b_\ell = -0.58 \pm 0.18\%$ cycle^{-1}) for BSSS(R)Cn and -7.57% cycle^{-1} ($b_\ell = -3.12 \pm 0.18\%$ cycle^{-1}) for BSCB1(R)Cn. For S_1 generation, the indirect response was -4.18% cycle^{-1} ($b_\ell = -0.46 \pm 0.25\%$ cycle^{-1}) for BSSS(R)Cn and -8.45% cycle^{-1} ($b_\ell = -2.05 \pm 0.18$) for BSCB1(R)Cn. In general, percentage of stalk lodging for populations per

se and interpopulation crosses in S_1 generation was approximately half of that in S_0 generation. The BSCB1(R)Cn population and the crosses that included BSCB1(R)Cn tended to have greater rates of response than BSSS(R)Cn and its crosses.

Ear height of S_0 and S_1 generations increased in the interpopulation crosses but decreased in populations per se (Table 6). The rates of response were approximately -0.80 cm cycle^{-1} for ear height in the S_0 generation of both parental populations and 0.37 cm cycle^{-1} in the S_0 generation of the interpopulation cross. Plant height also increased in the interpopulation cross in S_0 and S_1 generations (Table 7). The rate of increase in ear and plant height in S_1 generation of interpopulation cross was greater than that in S_0 generation.

Silking and pollen date increased in BSCB1(R)Cn and decreased in BSSS(R)Cn for both generations (Table 1). Silking date changed significantly in S_0 generation of the populations per se and the interpopulation cross (Table 8). A linear decrease of -0.35 $\pm$ 0.04 and -0.24 $\pm$ 0.04 days cycle^{-1} were observed in S_0 generation of BSSS(R)Cn and BSSS(R)Cn x BSCB1(R)Cn, respectively. The S_0 generation of BSCB1(R)Cn had a significant quadratic trend for silking date. Silking date in the S_0 generation of BSCB1(R)Cn increased from C0 to C4 followed by a gradual decrease after C4. A rapid decrease in silking date from C0 to C4 followed by slight decrease after C4 was observed in S_0 generation of BSSS(R)Cn. At the C4, silking dates were similar for S_0 generation of BSSS(R) (86.4 days) and BSCB1(R) (86.7 days). Significant quadratic trends in pollen date were observed in S_0 generation of BSSS(R)Cn and

BSCB1(R)Cn (Table 9). The change in pollen date for S_0 generation of BSSS(R)Cn x BSCB1(R)Cn was not significant. The rapid decrease of pollen date in S_0 generation of BSSS(R) and rapid increase of pollen date in S_0 generation of BSCB1(R) in the first four cycles were also detected.

DISCUSSION

RRS was effective for improving grain yield of BSSS(R)Cn x BSCB1(R)Cn interpopulation cross. After 11 cycles of selection, grain yield in the interpopulation cross increased 6.95% cycle^{-1}. Lower rates of response were observed in the populations per se. The BSCB1(R)Cn population showed greater response than the BSSS(R)Cn population. Although response was not significant in BSSS(R)Cn, a positive increase in grain yield of BSSS(R)Cn was observed. The greater response in the interpopulation cross has been realized for all studies of RRS in BSSS(R)Cn and BSCB1(R)Cn, but the magnitudes of response were not the same. Smith (1983) evaluated the response for two intervals (cycle 0-4 and 4-8) of the same RRS program. Responses for grain yield of the interpopulation cross were 0.247 $\pm$ 0.033 Mg ha^{-1} cycle^{-1} for cycles 0-4 and 0.361 $\pm$ 0.045 Mg ha^{-1} cycle^{-1} for cycles 4-8. These responses were greater than 0.118 Mg ha^{-1} cycle^{-1} reported by Penny and Eberhart (1971) and 0.175 Mg ha^{-1} cycle^{-1} reported by Martin and Hallauer (1980) but similar to 0.273 Mg ha^{-1} cycle^{-1} estimated by Eberhart et al. (1973). Smith (1983) pointed out that the rate of response in his study was greater because almost all trials were machine-harvested with no gleaning for dropped ears whereas the trials in the studies of Penny and Eberhart (1971) and Martin and Hallauer (1980) were hand harvested. The results of our study agree with those from Smith (1983). Machine-harvesting was used for all plots in our study and the estimate of 0.28 $\pm$ 0.02 Mg ha^{-1} cycle^{-1} in our study was comparable to that reported by Smith (1983).

In general, the changes in agronomic traits have been acceptable and

in the desired direction. Although not statistically significant in all instances, selection tended to decrease both root and stalk lodging for populations and crosses (Tables 4 and 5). Root lodging was nearly absent in BSSS(R)C11. The 0.2% root lodging observed for BSSS(R)C11 was lower than the average root lodging (5.6%) in the three single-cross checks. Rogers et al. (1977) indicated that variation for root lodging in BSSS was less than other populations. The results from our study suggested that the variation for root lodging was adequate and selection has increased the frequency of favorable alleles for root lodging in BSSS(R).

Selection has been effective in decreasing stalk lodging in BSCB1(R)Cn, although BSCB1(R)Cn was not initially synthesized from lines having above average stalk quality. Stalk lodging in BSCB1(R)Cn decreased from 40.4% in C0 to 9.7% in C11. The rate of response in BSCB1(R)Cn for stalk lodging was greater than that observed in BSSS(R)Cn. The greater response was also reflected in the testcrosses of BSCB1(R)Cn. However, stalk lodging in BSSS(R)Cn and BSSS(R)Cn x BSCB1(R)Cn did not show a decrease until after cycle 4 of selection. Although BSCB1(R)Cn showed a decrease in stalk lodging from C0 to C4, the greatest decrease occurred after the C4. This may have resulted from the change in selection criteria from hand-harvested yield to machine-harvested yield. The screening of S_1 plants before making testcrosses may also have increased response to selection for stalk lodging.

There were no major changes observed after selection for grain moisture at harvest. Grain moisture at C0 for the populations and their crosses was almost identical to grain moisture at C11 (Table 3). This

lack of change in grain moisture at harvest has been one of the objectives of selection. The direction of response was the same for plant and ear height. Plant and ear height decreased in populations per se and increased in population crosses. Ear height decreased in populations per se at a greater rate than plant height but increased in population crosses at a lower rate than plant height. Silking and pollen dates increased in BSCB1(R)Cn but decreased in BSSS(R)Cn and BSSS(R)Cn x BSCB1(R)Cn. There was about six days difference between BSSS(R)C0 and BSCB1(R)C0 for both silking and pollen dates. The changes in silking and pollen dates in populations per se would be a result of selection of plants in each population to produce the testcrosses.

Inbreeding depression tended to reduce grain yield, increase grain moisture, reduce plant and ear height, and delay flowering dates. There was no directional change from the S_0 to S_1 generation for root lodging but stalk lodging was decreased in S_1 generation.

The improvement after RRS for grain yield in BSSS(R)Cn and BSCB1(R)Cn per se, and testcrosses to their original parents (C0) indicated that the frequency of favorable alleles has increased at loci affecting grain yield in the selected populations. However, the estimated rates of linear response in BSSS(R)Cn and BSCB1(R)Cn per se were significantly less than those observed in the testcross of populations to their original parents (Table 2). The difference observed in the rates of response between the populations per se and their testcrosses to C0 were most likely the result of inbreeding depression due to small population size. Inbreeding depression as a result of

gentic drift was expected to occur because only 10 lines in the first eight cycles and 20 lines in the last three cycles were intermated to form populations in each cycle. The genetic drift may have caused fixation of unfavorable alleles, thus decreasing the observed gain in the populations. By the eleventh cycle, the expected inbreeding level in each population was at least 37%. The effect of decreasing favorable allele frequencies at some loci due to random genetic drift was partially offset by selection for increasing favorable allele frequencies at other loci. Consequently, grain yield of BSSS(R)Cn and BSCB1(R)Cn increased slightly. Smith (1983) indicated that inbreeding depression due to the small number of progenies selected for intermating in the BSSS(R)Cn and BSCB1(R)Cn population would explain the lack of response in the populations per se when compared to population crosses. He noted that after adjustment for the effects of genetic drift, the indirect effect of selection in the populations per se was greater than the direct effect of selection in the interpopulation cross. Helms et al. (1989) also reported that the effects of random genetic drift, which resulted in inbreeding depression were significant in BSSS(R)Cn.

The increases in grain yield of the testcrosses of BSSS(R)Cn with BSSS(R)C0 and BSCB1(R)C0, and the testcroses of BSCB1(R)Cn with BSSS(R)C0 and BSCB1(R)C0 along with the slight increases in grain yield of BSSS(R)Cn and BSCB1(R)Cn per se suggested that dominance was the major type of gene action involved. Both partial and complete dominance are possible explanations for the changes in the testcross performance.

RRS resulted in an increase in grain yield when BSSS(R)Cn was crossed to an unrelated (Mo17) and related (B73) inbred line. The

quadratic trend in BSSS(R)Cn x Mo17 was obtained because of a slight decrease in grain yield at C10 and C11 (Table 2). However, yield of BSSS(R)C11 x Mo17 was significantly greater than BSSS(R)C0 x Mo17. The linear response in grain yield was also observed for the crosses of BSCB1(R)Cn with the unrelated (B73) and related (Mo17) inbred lines. The results indicate that the populations have increased frequency of favorable alleles at loci complementary to the two inbred lines. The improvement in grain yield of the crosses of BSSS(R)Cn and BSCB1(R)Cn with both inbred lines also suggest that RRS was effective in improving the general as well as specific combining ability of populations per se. Rates of response were 1.94% cycle^{-1} for BSSS(R)Cn x B73 and 2.60% cycle^{-1} for BSSS(R)Cn x Mo17. Rates of response of BSCB1(R)Cn testcrosses with B73 and Mo17 were 2.67 and 3.78% cycle^{-1}, respectively. The difference between the rates of response in grain yield of populations testcrossed to related and unrelated inbred lines was not significant for either population. The improvement of the population testcrosses with the related inbred line [BSSS(R)Cn x B73 and BSCB1(R)Cn x Mo17] suggested that the effects of selection and random genetic drift were sufficient to create different allelic frequencies resulting in heterosis in the testcrosses.

There were no improvements in mean grain yield of the C10 x C10 and C11 x C11 interpopulation cross between BSSS(R)Cn and BSCB1(R)Cn (Table 2). Some evidence of a similar type of response in the populations per se was also observed. There is no clear-cut evidence explaining the lack of response. However, the change in method from reciprocal half-sib

selection to reciprocal full-sib selection after completing C9 may be contributing to the lack of response in C10 and C11. Both C10 and C11 of BSSS(R) and BSCB1(R) were formed based on the performance of reciprocal full-sib progenies. By using reciprocal full-sib progenies rather than half-sib progenies, the genetic variance among testcross progenies was expected to increase. However, Smith and Guy (1982) reported that the variance among the testcross progenies produced from BSSS(R)C9 and BSCB1(R)C9 was lower than expected. Consequently, the lack of response in the last two cycles of selection may be the result of reduced genetic variance. Another change, that may affect selection response, was that 20 rather than 10 lines were intermated to form C9, C10, and C11 populations. This change was made to reduce the cumulative effects of genetic drift and slow the rate of allele fixation. The 20 lines were selected from 100 prognies (20%) in C9, 160 progenies (12.5%) in C10, and 112 progenies (17.9%) in C11 of selection (Lamkey et al., 1991). When compared to selection of 10 lines from approximately 100 progenies (10%) in cycles 0-8, the change to 20 lines for intermating has also reduced the selection intensity, which will slow the rate of progress from selection (Lamkey et al., 1991).

Midparent heterosis for grain yield in the interpopulation crosses increased from 0.86 Mg ha^{-1} for the C0 x C0 cross to 2.92 Mg ha^{-1} for the C11 x C11 cross (Table 10). Heterosis expressed as a percentage of midparent increased from 25.44% to 76.04% after 11 cycles of selection (Table 11). Because grain yield of parental populations did not decrease with cycles of selection and their population cross increased in grain

yield at a greater rate, the increase in heterosis was primarily a result of the increase in grain yield of the population cross.

Inbreeding depression for grain yield in actual units for BSSS(R)Cn decreased from 1.15 Mg ha^{-1} in C0 to 0.64 Mg ha^{-1} in C11 (Table 12). However, inbreeding depression in BSCB1(R)Cn showed an inconsistent trend. Inbreeding depression in the interpopulation cross steadily increased from 1.01 Mg ha^{-1} (C0 x C0) to 2.32 Mg ha^{-1} (C11 x C11). The increased inbreeding depression coupled with increased heterosis in the interpopulation crosses observed over cycles of selection indicated that the crosses of improved populations have more heterozygous loci for grain yield than the cross of the original populations. The most likely explanation for the increased inbreeding depression and heterosis in the interpopulation crosses is that selection has been for alleles at complementary loci in each population. A divergence in the frequency of favorable alleles between the parental populations may also have been created by genetic drift by fixation of different alleles at a locus in each population which would also result in increased heterosis and inbreeding depression in the interpopulation crosses. However, if genetic drift fixed the same alleles at a locus in each population, heterosis may have increased but no change in inbreeding depression of the interpopulation crosses would have been observed. Another explanation for the increased inbreeding depression in the interpopulation cross is an increase in the number of segregating loci in the population cross. This explanation can be discarded because RRS has been performed with closed populations.

The results of this study indicated that RRS was effective for improving grain yield and the performance of other important agronomic traits in the population cross between BSSS(R)Cn and BSCB1(R)Cn. Lines extracted from improved populations could be used in hybrid combination to maximize heterotic effects. RRS also improved general as well as specific combining ability of the populations per se. As results of our study, it appears reasonable to conclude that RRS should be useful for producing improved germplasm sources for extraction of inbred lines for use in applied breeding program. The lines extracted from the improved populations would be better in their combining ability with lines from Lancaster Sure Crop and Reid Yellow Dent germplasms.

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SECTION II. EFFECTS OF SELECTION AND GENETIC DRIFT ON RESPONSE TO RECIPROCAL RECURRENT SELECTION IN BSSS AND BSCB1 MAIZE POPULATIONS

ABSTRACT

Reciprocal recurrent selection (RRS) has the advantage of capitalizing on both additive and non-additive genetic effects. It was designed to improve the cross between two populations by complementary changes of allelic frequencies in both populations. Eleven cycles of RRS have been completed in BSSS and BSCB1 maize populations. The objectives of this study were to partition the response to selection into that due to additive and dominance genetic effects and to evaluate the effects of genetic drift using a model proposed by Smith (1983). A population diallel of the C0, C4, C7, C9, and C11 cycles of BSSS(R) and BSCB1(R) and the C8 and C10 interpopulation crosses of BSSS(R) and BSCB1(R) were evaluated. The populations per se selfed and interpopulation crosses selfed involving the C0, C4, C7, C8, C9, C10, C11 cycles of the populations were included in the study.

Mean performances of the BSSS(R)C0 and BSCB1(R)C0 for grain yield, ear height, plant height, silking date, and pollen date were mainly controlled by additive genetic effects. On the other hand, the contribution of dominance effects appears to be more important in performance of stalk lodging in BSSS(R)C0 and BSCB1(R)C0.

The estimated genetic parameters indicate that selection effectively increased frequency of favorable alleles affecting grain yield in the improved populations. Responses to selection for grain yield resulted from changes in frequency of alleles having both additive and dominance effects in BSSS(R) and primarily dominance effects in BSCB1(R). Acceptable changes were also observed in most evaluated traits. Genetic

drift effects due to finite population size were significant for grain yield and plant height in both populations, ear height in BSCB1(R), and silking and pollen date in BSSS(R). Significant heterosis between BSSS(R) and BSCB1(R) was observed for grain yield, plant height, ear height, and pollen date.

It is evident that the effects of inbreeding due to genetic drift for grain yield, which were similar for both populations, would limit the improvement in the populations per se that can be achieved by selection. The estimated indirect responses in the populations per se, adjusted for the effects of genetic drift, were similar to the estimated direct response in the interpopulation cross. The effects of finite population size should be considered in the RRS program if the objective of selection is to increase favorable alleles at most loci and maintain genetic variability in the populations.

INTRODUCTION

Because heterosis is expected in commercial maize (Zea mays L.) hybrids, parallel improvement of two populations that maximizes heterosis in their cross would be of importance. The simultaneous improvement of two populations, known as reciprocal recurrent selection (RRS), was originally proposed by Comstock et al. (1949) to emphasize selection for both additive and non-additive genetic effects. Reciprocal recurrent selection is expected to be effective for developing germplasm sources for hybrid maize breeding programs because selection is based on the performance of the interpopulation cross where any type of gene action has opportunity for expression. Both general and specific combining ability of populations per se would be improved in the advanced cycles of selection, thus increasing the chance of obtaining inbred lines with better combining ability.

A RRS program was initiated in 1949 in Iowa with two populations: 'Iowa Stiff Stalk Synthetic' (BSSS) and 'Iowa Corn Borer Synthetic No. 1' (BSCB1). Reports of progress achieved with RRS were presented periodically (Penny and Eberhart, 1971; Eberhart et al., 1973; Martin and Hallauer, 1980; Smith, 1983; Helms et al., 1989; Keeratinijakal and Lamkey, 1990). In general, the direct response of selection in the interpopulation cross was greater than the indirect responses observed in the populations per se. Smith (1979, 1983) proposed a model that permits partitioning the response from selection into components due to additive and dominance gene effects. The model also allows estimation of the effects genetic drift due to finite population size. Smith (1983) used

the model to evaluate response to selection in BSSS(R) and BSCB1(R) population after seven cycles of RRS. He found that the indirect responses adjusted for the effects of genetic drift were larger than the direct response. Effects of genetic drift due to small population size in BSSS(R) were also detected by Helms et al. (1989). Although genetic drift results in a lack of response in the populations of per se, empirical studies have shown that genetic drift does not affect the response of the interpopulation cross which is the primary objective of a RRS program.

The objectives of this study were to partition the response to selection in BSSS(R) and BSCB1(R) into that due to additive and dominance gene effects and to evaluate the effects of genetic drift on the indirect response observed in the populations per se.

MATERIALS AND METHODS

The details of the first five cycles of selection in RRS program in Iowa with the BSSS and BSCB1 were presented by Penny and Eberhart (1971). The details of changes that have been made in the selection program, since the initiation of the program in 1949, were described by Keeratinijakal and Lamkey (1990).

In the 1987 breeding nursery at the Agronomy and Agricultural Engineering Research Center near Ames, Iowa, a population diallel was produced among the C0, C4, C7, C9, and C11 cycles of BSSS(R) and BSCB1(R). In addition, the C8 and C10 interpopulation crosses of BSSS(R) and BSCB1(R) were produced. Seed of the C0, C4, C7, C8, C9, C10, and C11 of BSSS(R) and BSCB1(R) populations per se, populations per se selfed, and testcrosses of the populations to inbred lines B73 and Mo17 were also produced. Selfed seed of the C0, C4, C7, C8, C9, C10, and C11 interpopulation crosses was produced in the 1988 nursery. The populations per se, populations per se selfed and interpopulation crossses selfed were produced by intercrossing or selfing approximately 100 plants. The population crosses were produced by reciprocally crossing 50 plants from each population. Testcrosses of the populations to the inbred lines were produced by sampling 50 plants as males or females from the populations.

The noninbred and inbred material were evaluated in separate experiments grown at four Iowa locations (Ames, Ankeny, Martinsburg, and Clarence) in 1988 and 1989. Data were not obtained from the Clarence location in 1989 due to the residual effects of herbicides used on the

soybean [Glycine max (L.) Merrill] crop grown the previous year. The entries included in the noninbred experiment were the 47 population crosses, 14 populations per se, 28 testcrosses, and 14 checks. Duplicate entries of the BSSS(R)C0 and BSCB1(R)C0 populations per se and the C0 x C0, C4 x C4, C7 x C7, C9 x C9, and C11 x C11 interpopulation crosses between BSSS(R) and BSCB1(R) were also included for a total of 110 entries. The 110 entries were evaluated in a 10 x 11 triple rectangular-lattice design. The entries included in the inbred experiment were the 14 populations per se selfed in 1988 and the 14 populations per se selfed plus the seven interpopulation crosses selfed in 1989. The inbred entries were evaluated in a randomized complete-block design with three replications.

Plots were two-rows 5.49 m long with 0.76 m between rows. All plots were overplanted and thinned to a uniform stand. Stand density was approximately 62,190 plants ha^{-1} for the 1988 experiments and 52,600 plants ha^{-1} for the 1989 experiments. All experiments were machine-planted and harvested with no gleaning of dropped ears. Data for grain yield (Mg ha^{-1} at 15.5% grain moisture), grain moisture (%), stand (plants ha^{-1}), stalk lodging (% plants broken below the ear node), and root lodging (% plants inclined more than 30^{o} from vertical) were collected from seven experiments. Ear height (cm) and plant height (cm) were obtained from five experiments. Ear and plant height were calculated as the average of measurements on ten competitive plants per plot and measured as the distance from the soil surface to highest ear bearing node (ear height) and the node of the flag leaf (plant height). Silking

date and pollen date were recorded as the number of days from planting to 50% silk emergence and 50% pollen shed, respectively. Silking and pollen date were recorded at the Ames location in 1988 and 1989.

Means of noninbred genotypes adjusted for lattice block effects and means of inbred genotypes were combined into one data set. This data set included means of BSSS(R)Cn and BSCB1(R)Cn population per se; BSSS(R)Cn x BSCB1(R)Cn interpopulation crosses; BSSS(R)Cn x BSSS(R)Cn, BSCB1(R)Cn x BSCB1(R)Cn and BSSS(R)Cn x BSCB1(R)Cn population crosses; BSSS(R)Cn and BSCB1(R)Cn population per se selfed; and BSSS(R)Cn x BSCB1(R)Cn interpopulation crosses selfed for a total of 82 entries. Means in the data set were used to estimate genetic parameters in the model described by Smith (1983). The model was used to estimate the contribution of additive and dominance gene effects to the response to selection and also allow the estimation of the effects of genetic drift due to small population size. The genetic parameters involved in the model for each population were the following:

AOI = contribution of homozygous or additive effects to the mean of the I^{th} base population = $\Sigma(2p-1)a + \mu$,

DOI = contribution of heterozygous or dominance effects to the mean of the I^{th} base population = $\Sigma p(1-p)d$,

ALI = the partial linear regression coefficient of the changes in allelic frequencies and additive effects in the I^{th} population or one-half the change in the population mean due to the effect of homozygous loci on a per cycle basis = $\Sigma\Delta pa$,

DLI = the partial linear regression coefficient of the changes in allelic frequencies and dominance effects in the I^{th} population or one-half the change in the population mean due to the effect of heterozygous loci on a per cycle basis = $\Sigma\Delta p(1-2p)d$,

DQI = the partial quadratic regression coefficient of the changes in allelic frequencies and dominance effect in the I^{th} population or one-half the change in the population mean after one cycle of selection due to the effect of finite population size if effective population size is less than or equal to 25 = $\Sigma(\Delta p)^2 d$,

DLII' = the partial linear regression coefficient of the changes in allelic frequencies, the difference in initial allelic frequencies, and dominance effects due to the I^{th} population in the cross of the I^{th} and I^{th}-prime population or one-half the contribution of the I^{th} population to the change in mean of the cross of the I^{th} and I^{th}-prime populations = $\Sigma\Delta p(p-p')d$,

HII' = heterosis in the cross of the C0 of I^{th} and I^{th}-prime populations when $I \neq I'$ = $\Sigma(p-p')d$,

HQII' = the partial quadratic regression coefficient of the changes in allelic frequencies and dominance effects in the cross of the I^{th} and I^{th}-prime populations when $I \neq I'$ = $\Sigma\Delta p\Delta p'd$,

where

μ = the mean of the base genotype or the contribution to the mean

of those loci which are fixed in the population;

a = the coded genotypic value of homozygous genotype;

d = the coded genotypic value of heterozygous genotype;

p = the initial frequency of a favorable allele (G_i) at the i^{th} locus in population I;

p' = the initial frequency of the G_i allele at the i^{th} locus in population I';

$\bar{p}$ = the change in allelic frequency in population I after one cycle of selection for the G_i allele; and

$\bar{p}'$ = the change in allelic frequency in population I' after one cycle of selection for the G_i allele.

Genetic parameters ($\hat{\beta}$) were calculated by using weighted least squares: $\hat{\beta} = (X'W^{-1}X)^{-1}X'W^{-1}Y$; where the elements of the Y-matrix are the entry means and the elements of the X-matrix are functions of cycle number and the coefficients of the genetic parameters. W is a matrix with the variances of the cycle means on the diagonal and zeros on the off diagonal. Standard errors of the parameter estimates were calculated as the square root of the corresponding diagonal element (C_{ii}) of the $(X'W^{-1}X)^{-1}$ matrix.

RESULTS AND DISCUSSION

The least square estimates of the genetic parameters of the model (Smith, 1983) for all traits are presented in Tables 1 to 4. For grain yield, the contribution of the additive effects to the mean of C0 population (A0I) was significantly different from zero for BSSS(R) and BSCB1(R) (Table 1). Significant estimates of dominance effects (D0I) were observed for both populations, but the effects were small relative to the respective A0I terms. This indicates that grain yield in BSSS(R)C0 and BSCB1(R)C0 was controlled by alleles with additive and dominance effects. The larger A0I estimates suggests that grain yield was largely controlled by alleles with additive effects. If the average frequency of favorable alleles (p_i) for grain yield in the base population was equal to 0.5, A0I would be near zero and nonsignificant, and D0I would attain its maximum value. The average frequency of favorable alleles in the base populations, BSSS(R) and BSCB1(R), must not be 0.5 or near 0.5 because the A0I estimate was significantly different from zero and relatively larger than the D0I estimate in each population.

A significantly larger estimate of D0I for BSSS(R) compared to BSCB1(R) indicates that average frequency of favorable alleles affecting grain yield was larger in BSSS(R)C0 than in BSCB1(R)C0. The larger initial frequency of favorable alleles in BSSS(R) was reflected in the greater observed mean grain yield of BSSS(R)C0 compared to BSCB1(R)C0 (Table 5). Furthermore, the BSSS(R)C0 had greater inbreeding depression for grain yield than BSCB1(R)C0 (Keeratinijakal and Lamkey, 1990) which could also be interpreted as the result of larger D0I estimate in

Table 2. Least squares estimates of genetic parameters (Smith, 1983) of the BSSS(R) and BSCB1(R) populations for root and stalk lodging

Trait	Parameter	Population	
		BSSS(R)	BSCB1(R)
Root lodging	AOI	4.681 ± 3.489	6.013 ± 3.489
(%)	DOI	0.719 ± 2.105	3.653 ± 2.105
	ALI	-0.093 ± 0.224	0.026 ± 0.224
	DLI	0.039 ± 0.329	-0.550 ± 0.329
	DQI	-0.011 ± 0.017	0.019 ± 0.017
	DLII'	-0.055 ± 0.143	0.110 ± 0.143
	HII'	0.107 ± 0.846	
	HQII'	0.008 ± 0.014	
	R^2	0.945	
Stalk lodging	AOI	1.396 ± 2.976	6.306 ± 2.976*
(%)	DOI	9.376 ± 1.841**	17.635 ± 1.841**
	ALI	-0.154 ± 0.192	-0.451 ± 0.192*
	DLI	-0.155 ± 0.294	-1.096 ± 0.294**
	DQI	0.002 ± 0.015	-0.003 ± 0.015
	DLII'	0.086 ± 0.132	0.319 ± 0.132*
	HII'	-1.445 ± 0.777	
	HQII'	-0.021 ± 0.012	
	R^2	0.984	

*,**Significantly different at the 0.05 and 0.01 probability levels, respectively.

Table 3. Least square estimates of genetic parameters (Smith, 1983) of the BSSS(R) and BSCB1(R) populations for ear and plant heights

Trait	Parameter	Population	
		BSSS(R)	BSCB1(R)
Ear height	AOI	66.972 ± 2.989**	65.657 ± 2.989**
(cm)	DOI	22.598 ± 1.751**	19.067 ± 1.751**
	ALI	0.298 ± 0.192	-0.093 ± 0.192
	DLI	-0.514 ± 0.269	0.305 ± 0.269
	DQI	-0.018 ± 0.013	-0.068 ± 0.013**
	DLII'	0.054 ± 0.112	-0.022 ± 0.112
	HII'	2.916 ± 0.660**	
	HQII'	0.014 ± 0.010	
	R^2	0.999	
Plant height	AOI	146.961 ± 3.985**	152.717 ± 3.985**
(cm)	DOI	33.560 ± 2.315**	25.560 ± 2.315**
	ALI	1.276 ± 0.256**	-0.120 ± 0.256
	DLI	-0.912 ± 0.354*	1.211 ± 0.354**
	DQI	-0.047 ± 0.017**	-0.131 ± 0.017**
	DLII'	0.101 ± 0.146	-0.203 ± 0.146
	HII'	4.168 ± 0.857**	
	HQII'	0.018 ± 0.014	
	R^2	0.999	

*,**Significantly different at the 0.05 and 0.01 probability levels, respectively.

Table 4. Least square estimates of genetic parameters (Smith, 1983) of the BSSS(R) and BSCB1(R) populations for silking and pollen date

Trait	Parameter	Population	
		BSSS(R)	BSCB1(R)
Silking date	AOI	93.468 ± 1.012**	92.047 ± 1.012**
(days)	DOI	-2.330 ± 0.565**	-4.183 ± 0.565**
	ALI	-0.011 ± 0.064	0.054 ± 0.064
	DLI	-0.267 ± 0.084**	0.064 ± 0.084
	DQI	0.009 ± 0.004*	-0.004 ± 0.004
	DLII'	-0.028 ± 0.033	-0.091 ± 0.033**
	HII'	-0.005 ± 0.189	
	HQII'	0.009 ± 0.003**	
	R^2	0.999	
Pollen date	AOI	88.162 ± 1.076**	85.588 ± 1.076**
(days)	DOI	-1.553 ± 0.577**	-2.981 ± 0.577**
	ALI	0.015 ± 0.069	0.099 ± 0.069
	DLI	-0.235 ± 0.081**	0.078 ± 0.081
	DQI	0.014 ± 0.003**	-0.003 ± 0.003
	DLII'	0.038 ± 0.026	-0.064 ± 0.026*
	HII'	-0.342 ± 0.155*	
	HQII'	0.004 ± 0.002*	
	R^2	0.999	

*,**Significantly different at the 0.05 and 0.01 probability levels, respectively.

Table 5. Mean grain yields across environments for populations, population cross, and their S_1 generation (lower value)

	BSSS(R)						
	C0	C4	C7	C8	C9	C10	C11
	Mg ha^{-1}						
BSSS(R)C0	3.55[a,b] 2.40						
BSSS(R)C4	4.00	3.76 2.88					
BSSS(R)C7	4.54	4.60	4.24 2.83				
BSSS(R)C8	--[c]	--	--	4.34 3.34			
BSSS(R)C9	4.92	4.98	4.47	--	4.25 3.39		
BSSS(R)C10	--	--	--	--	--	3.98 3.22	
BSSS(R)C11	4.84	4.69	4.41	--	4.07	--	3.92 3.28
BSCB1(R)C0	4.24[a] 3.41	4.16	5.10	--	5.20	--	5.51
BSCB1(R)C4	4.37	4.94[a] 4.40	5.36	--	5.64	--	5.66
BSCB1(R)C7	4.96	5.74	6.08[a] 5.13	--	6.63	--	6.35
BSCB1(R)C8	--	--	--	6.59[a] 5.39	--	--	--
BSCB1(R)C9	5.50	6.32	6.42	--	6.94[a] 5.38	--	6.70
BSCB1(R)C10	--	--	--	--	--	6.84[a] 5.47	--
BSCB1(R)C11	5.86	6.62	6.62	--	6.95	--	6.76[a] 5.09

[a]Mean of duplicated entries.

[b]S.E. of means are 0.24 for S_0 population, 0.17 for S_1 population, 0.21 for S_1 population cross and 0.17 for duplicated entries of S_0 population.

[c]Not included in the study.

BSCB1(R)						
C0	C4	C7	C8	C9	C10	C11
Mg ha^{-1}						
3.21[a] 2.55						
3.48	3.16 2.83					
4.14	3.95	3.61 2.52				
--	--	--	3.30 2.62			
4.92	4.28	3.96	--	3.87 2.74		
--	--	--	--	--	3.59 2.92	
4.81	4.39	4.02	--	4.02	--	3.76 2.80

BSSS(R)C0 due to the larger frequency of favorable alleles.

Changes in allelic frequencies due to additive (ALI) and dominance effects (DLI) in BSSS(R) were significant for grain yield. The positive value of the ALI and DLI estimates in BSSS(R) indicates that RRS effectively increased the frequency of favorable alleles in the BSSS(R) with additive and dominance effects. In BSCB1(R), the estimate of ALI was not significant whereas the DLI estimate was positive and significant. The changes in allelic frequencies due to selection in BSCB1(R) occurred mainly at loci having alleles with dominance effects. The small estimate of ALI and large estimate of DLI in BSCB1(R) indicates that improvement in grain yield of BSCB1(R) population was greater than improvement in the BSCB1(R) population selfed. The estimated rates of response in grain yield of 0.06 Mg ha^{-1} $cycle^{-1}$ for BSCB1(R) population and 0.02 Mg ha^{-1} $cycle^{-1}$ for BSCB1(R) population selfed (Keeratinijakal and Lamkey, 1990) support this interpretation.

If the initial allelic frequencies are intermediate, DLI is not significantly different from zero because the term $(1-2p_i)$ is equal to zero when $p_i = 0.5$ (Smith, 1979). Thus, the significant estimates of DLI for BSSS(R) and BSCB1(R) suggests that the initial allelic frequencies must deviate significantly from 0.5. The larger estimate of DLI for BSCB1(R) relative to BSSS(R) indicates a lower frequency of favorable alleles in BSCB1(R), assuming that changes in frequency of favorable alleles after one cycle of selection (Δp_i) in both populations were small.

The effect of loss of heterozygotes in the populations per se due to finite population size (DQI) in both populations was similar (-0.012 $\pm$

0.002 Mg ha^{-1} $cycle^{-1}$) and significantly different from zero ($p < 0.01$). The negative estimates of DQI in both populations suggests that inbreeding due to genetic drift limited the improvement in the populations per se that can be achieved by selection. Both populations would have accumulated inbreeding at a similar rate. The similar rate of inbreeding depression could be the consequence of the effective population size which was similar for both populations in each cycle of selection.

Estimates of DLII' are the linear changes due to contributions of heterozygous loci in BSSS(R) and BSCB1(R) to the BSSS(R) x BSCB1(R) population cross. Estimates of DLII' for grain yield were not significant for either population, which indicates that improvement in the population cross was dependent largely on the improvement in the populations per se (ALI + DLI).

The effect due to heterosis (HII') was significant ($p < 0.01$) indicating that there was directional dominance for grain yield and a divergence in the frequency of alleles affecting grain yield between original populations. The estimate of HQII' for grain yield was equal to zero. The HQII' estimate can be defined in relation to allelic frequencies and allelic effects as $\Sigma\Delta p\Delta p'd$. If directional dominance does not exist, the HQII' term would not be significantly different from zero. However, the significant estimates of DOI, DLI, and HII' in the populations indicates the existence of directional dominance for grain yield. Thus, the zero value for HQII' estimate can be explained by the following: (1) if the change in allelic frequencies in one population

was equal to zero; or (2) if allelic frequencies for some loci were changed in one direction and the allelic frequencies at other loci were changed in the opposite direction in one or both populations, their effects over all loci would tend to cancel out (Tanner and Smith, 1987). These explanations also verify that RRS may select favorable alleles with dominance effects at the different loci in each population. Consequently, the steady increase in inbreeding depression and heterosis in the interpopulation crosses with cycles of selection (Keeratinijakal and Lamkey, 1990) would also suggest selection for favorable alleles at the different loci in each population.

The realized gains for grain yield in the populations per se [2(ALI + DLI)], which are the indirect responses adjusted for the effects of genetic drift, were significant for both populations (Table 6). The realized gains were similar for BSSS(R) and BSCB1(R) populations with the rates of 0.295 $\pm$ 0.041 Mg ha^{-1} $cycle^{-1}$ and 0.297 $\pm$ 0.041 Mg ha^{-1} $cycle^{-1}$, respectively. The direct effects of selection (ALI + DLI + DLII') were significant in BSSS(R) (0.132 $\pm$ 0.014 Mg ha^{-1} $cycle^{-1}$) and BSCB1(R) (0.158 $\pm$ 0.014 Mg ha^{-1} $cycle^{-1}$). This indicates that improvement in the population cross was contributed by both populations. The estimated realized gain in the population crosses calculated from the sum of the direct effects of both populations was significant at 0.290 $\pm$ 0.022 Mg ha^{-1} $cycle^{-1}$ which is consistent with the observed rate of 0.280 $\pm$ 0.020 Mg ha^{-1} $cycle^{-1}$ in the population crosses reported by Keeratinijakal and Lamkey (1990). The realized gains for populations per se after adjusting for effects of genetic drift were not significantly different from the

Table 6. Least squares estimates of genetic model parameters (Smith, 1983) for eight traits in BSSS(R) and BSCB1(R) populations

		Traits		
		Grain		Root
		Yield	Moisture	lodging
		Mg ha^{-1}	----------%	----------
AOI	BSSS(R)	1.568**	21.411**	4.681
DOI	BSSS(R)	0.921**	-0.159	0.719
2(ALI + DLI)	BSSS(R)	0.295**	-0.063	-0.108
ALI + DLI + DLII'	BSSS(R)	0.132**	0.055*	-0.109
DQI	BSSS(R)	-0.012**	0.002	-0.011
AOI	BSCB1(R)	2.236**	18.725**	6.013
DOI	BSCB1(R)	0.373*	-0.616	3.653
2(ALI + DLI)	BSCB1(R)	0.297**	0.010	-1.047**
ALI + DLI + DLII'	BSCB1(R)	0.158**	0.019	-0.413**
DQI	BSCB1(R)	-0.012**	0.001	0.019
HII' [BSSS(R) X BSCB1(R)]		0.457**	-0.301	0.107
HQII' [BSSS(R) X BSCB1(R)]		0.000	0.002	0.008

*,**Significantly different at the 0.05 and 0.01 probability levels, respectively.

Traits				
Stalk lodging	Height		Date	
	Ear	Plant	Silking	Pollen
%	cm		days	
1.396	66.972**	146.961**	93.468**	88.162**
9.376**	22.598**	33.560**	-2.330**	-1.553**
-0.620*	-0.433	0.729	-0.557**	-0.440**
-0.223	-0.162	0.465**	-0.306**	-0.182**
0.002	-0.018	-0.047**	0.009*	0.014**
6.306*	65.657**	152.717**	92.047**	85.588**
17.635**	19.067**	25.560**	-4.183**	-2.981**
-3.095**	0.423	2.183**	0.236*	0.355**
-1.229**	0.189	0.889**	0.027	0.114**
-0.003	-0.068**	-0.131**	-0.004	-0.003
-1.445	2.916**	4.168**	-0.005	-0.342*
-0.021	0.014	0.018	0.009**	0.004*

realized gain for population crosses. Hence, lack of response in the observed grain yield of BSSS(R) and BSCB1(R) populations (Keeratinijakal and Lamkey, 1990) was due to inbreeding depression associated with genetic drift. Effects of genetic drift would confound effects of selection and limit the genetic potential in grain yield of the populations. At cycle 11, the estimated losses of grain yield due to effects of genetic drift ($2DQI \times n^2$) was 2.904 Mg ha^{-1} for both populations. The estimated reduction in grain yield due to effects of genetic drift for each cycle of selection included in this study is presented in Table 7.

The response per cycle of the testcross of the improved populations with the original population (Cn x C0) can be defined in relation to the model as ALI + DLI. The rates of responses were significant and similar for BSSS(R)Cn x BSSS(R)C0 and BSCB1(R)Cn x BSCB1(R)C0 (0.148 ± 0.021 Mg ha^{-1} $cycle^{-1}$). Apparently, RRS increased the frequency of favorable alleles of loci controlling grain yield in each population. The rates of responses in these testcrosses were half of the estimated realized gain in population cross. Keeratinijakal and Lamkey (1990) also found a similar pattern of responses in the testcrosses.

Grain moisture has been one of the traits considered in the selection program. Estimates of AOI for grain moisture were significant for both populations, but estimates of DOI were not significant for either population (Table 1). Comparisons between estimates of AOI and DOI in each population were significantly different suggesting that the trait was mainly controlled by additive effects. There was no

Table 7. Observed grain yield, predicted grain yield from the model (Smith, 1983) and predicted grain yield adjusted for genetic drift in original and improved populations of the BSSS(R) and BSCB1(R)

Populations	Observed yield	Predicted yield[a]	Yield adjusted for DQI	$2DQI(n)^2$
	----------	Mg ha^{-1}	----------	
BSSS(R)C0	3.55	3.41	3.41	0.00
BSSS(R)C4	3.76	4.21	4.59	0.38
BSSS(R)C7	4.24	4.31	5.49	1.18
BSSS(R)C8	4.34	4.25	5.79	1.54
BSSS(R)C9	4.25	4.14	6.08	1.94
BSSS(R)C10	3.98	3.98	6.38	2.40
BSSS(R)C11	3.92	3.77	6.67	2.90
BSCB1(R)C0	3.21	2.98	2.98	0.00
BSCB1(R)C4	3.16	3.79	4.17	0.38
BSCB1(R)C7	3.61	3.89	5.07	1.18
BSCB1(R)C8	3.30	3.84	5.38	1.54
BSCB1(R)C9	3.87	3.73	5.67	1.94
BSCB1(R)C10	3.59	3.58	5.98	2.40
BSCB1(R)C11	3.76	3.38	6.28	2.90

[a]Estimated as AOI + DOI + 2DOI + 2ALI(n) + 2DLI(n) + $2DQI(n^2)$, where n is the number of cycles of selection.

improvement in grain moisture over cycles of selection in either population as seen by the nonsignificant estimates of ALI and DLI. The effects of genetic drift over cycles of selection were not important for grain moisture in either population. It seems that there was no changes in allelic frequencies at loci affecting grain moisture. This was expected because high yielding testcross progenies in the evaluation trials without high grain moisture at harvest were selected in each cycle of selection. The results in this study suggest that RRS successfully maintained grain moisture while increasing grain yield. The heterosis term (HII') was significant for grain moisture indicating a difference in allelic frequencies between the base populations and some level of directional dominance.

All estimates of genetic parameters for root lodging were nonsignificant for both populations (Table 2). Estimates of AOI could be nonsignificant if frequency of alleles with additive effects for all loci (p_i) was 0.5 and mean of the base genotype (μ) was small. Estimates of ALI and other parameters related to dominance could be nonsignificant if there were no changes in allelic frequencies (Δp_i) and/or no directional dominance. However, the observed linear decreases in root lodging in BSSS(R) and BSCB1(R) (Keeratinijakal and Lamkey, 1990) suggests that selection reduced unfavorable alleles for root lodging. Thus, it seems that an appropriate explanation for the nonsignificant estimates of genetic parameters in this data set is that the model may not be sensitive enough to detect the small changes in allelic frequencies that occurred in both populations. Nevertheless, linear combination of the

parameters, 2(ALI + DLI) and ALI + DLI + DLII' were negative and significantly different from zero for BSCB1(R) (Table 6). This indicates that there was realized gain for root lodging in BSCB1(R) and that BSCB1(R) when crossed to BSSS(R) tended to decrease root lodging in the population cross. The linear combination of the parameters, however, was not significant in the BSSS(R) population.

For stalk lodging, estimates of DOI were significant for BSSS(R) and BSCB1(R), but estimates of AOI were significant only in BSCB1(R) (Table 2). Heterozygotes largely contribute to the appearance of stalk lodging in the original populations, although additive effects seem to have some contributions in BSCB1(R)C0. The larger estimates of AOI and DOI in BSCB1(R) compared to BSSS(R) reveals that frequency of unfavorable alleles in BSCB1(R)C0 were greater than in BSSS(R)C0. The observed stalk lodging means of 19.8% in BSSS(R)C0 and 40.9% in BSCB1(R)C0 (Keeratinijakal and Lamkey, 1990) also confirms this expectation.

In BSSS(R), changes in frequency of unfavorable alleles with additive and dominance effects were small as shown by nonsignificant estimates of ALI and DLI. However, the realized gain in BSSS(R) was significant (Table 6) indicating that stalk lodging was decreased over cycles by the effects of selection. The significant and negative estimates of ALI and DLI in BSCB1(R) population reveals that improved populations had less percentage of stalk lodging due to the contributions of additive and dominance effects. The major reduction of stalk lodging in BSCB1(R) was caused by the contributions of heterozygotes (DLI > ALI). Realized gain estimated from 2(ALI + DLI) for stalk lodging was

significantly greater in BSCB1(R) than BSSS(R). It seems that selection tended to decrease the frequency of unfavorable alleles in BSCB1(R) at a faster rate than BSSS(R). This would be expected because BSCB1(R)C0 had approximately two times as much stalk lodging as BSSS(R)C0. Apparently, RRS effectively reduced percentage of stalk lodging in BSCB1(R).

The estimates of D0I and DLI were significantly larger than A0I and ALI estimates in BSCB1(R), respectively, which indicates that the rate of response for stalk lodging in the populations per se was greater than that in the populations per se selfed. This is consistent with results reported by Keeratinijakal and Lamkey (1990). They reported rates of response of -3.12 ± 0.18 % cycle^{-1} for noninbred populations of BSCB1(R) and -2.05 ± 0.18 % cycle^{-1} for inbred populations of BSCB1(R).

Effects of genetic drift for stalk lodging were nonsignificant for both populations. Estimates of DLII' were significant only in BSCB1(R) suggesting that changes in the interpopulation cross were contributed partly by heterozygous loci in BSCB1(R) when crossed with BSSS(R). The positive estimate of DLII' indicates that direct effect (ALI + DLI + DLII') in BSCB1(R) in crosses with the BSSS(R) was less than the indirect effect (ALI + DLI) in the BSCB1(R) population per se.

The HII' estimate was not significant for stalk lodging, although other genetic parameters demonstrated the existence of initial genetic divergence between populations. However, the HII' estimate was significant at 0.10 probability level. There would be the difference in initial allelic frequencies between populations but the difference may not be large enough to be detected by the model. The estimate of HQII'

was not significant. Changes in allelic frequencies for alleles with dominance effects in BSSS(R) would be very small and attributed to the lack of significant in HQII' term.

The significant in AOI and DOI parameters for ear height in both populations (Table 3) suggests that ear height was controlled by alleles with additive as well as dominance effects. Alleles with dominance effects seemed to contribute less to ear height than alleles with additive effects in the base populations. Contributions to the genetic gains due to alleles with additive and dominance effects (ALI and DLI) were nonsignificant for both populations. The response of populations per se adjusted for genetic drift effects [2(ALI + DLI)] and direct effects (ALI + DLI + DLII') for BSSS(R) and BSCB1(R) were not significant (Table 6). Estimates of DQI were significant only in BSCB1(R) indicating that a loss of heterozygotes occurred and led to the reduction in ear height in BSCB1(R).

The expression of plant height in the base population of BSSS(R) and BSCB1(R) was also controlled by alleles with additive and dominance effects (Table 3). As with ear height, the effects of dominant alleles were less than the effects of additive alleles in the base populations. Changes in plant height over cycles of selection due to dominance effects were observed in both populations but the changes were in opposite directions. Frequency of dominant alleles that tend to increase plant height was decreased in BSSS(R) but increased in BSCB1(R). Changes in frequency of alleles with additive effects (ALI) increased plant height in BSSS(R) but no significant changes in alleles with additive effects

over cycles of selection was observed in BSCB1(R).

The direct effects of selection in BSSS(R) and BSCB1(R) measured by the linear combination ALI + DLI + DLII' were positive and significant (Table 6), which indicates that significant increases in plant height in the population crosses were contributed by both populations. The realized gain in the populations per se [2(ALI + DLI)] was significant only for BSCB1(R). The positive sign of the 2(ALI + DLI) indicates that selection tended to increase plant height in BSCB1(R). However, the significant DQI terms in both populations suggests that genetic drift effects also decreased plant height over cycles of selection. The estimated reduction of plant height due to genetic drift effects in cycle 11 were 11.37 cm in BSSS(R) and 31.70 cm in BSCB1(R).

Initial genetic diversity existed for ear and plant height because heterosis (HII') was significant for both characters. Estimates of HQII' for ear and plant height were not significant which indicates lack of significant changes in heterosis between BSSS(R)Cn and BSCB1(R)Cn. The lack of change in estimates of HQII' also suggests that selection may act at different loci in each population for ear and plant height.

Silking and pollen dates in BSSS(R)C0 and BSCB1(R)C0 were controlled by additive (A0I) and dominance (D0I) effects (Table 4). The significant difference between estimates of A0I and D0I for both characters indicates a larger contribution of additive effects compared with dominance effects. The negative estimate of D0I for silking and pollen dates suggests that heterozygotes tended to decrease days to flowering in the base populations.

In BSSS(R), estimates of ALI were not significant but estimates of DLI were negative and significant for both characters. This indicates that reductions in silking and pollen dates over cycles of selection in BSSS(R) were due to changes in frequency of alleles with dominance effects. The indirect responses of BSSS(R) after adjusting for effects of genetic drift [2(ALI + DLI)] (Table 6) were negative and significant indicating that the BSSS(R) population became earlier for silk emergence and pollen shedding due to effects of selection.

For BSCB1(R), estimates of ALI and DLI were nonsignificant for both characters. Nevertheless, the indirect responses 2(ALI + DLI) of BSCB1(R) showed significant increases in days to silk and pollen shedding. Hence, changes in allelic frequencies at loci affecting silking and pollen dates occurred with cycles of selection in BSCB1(R), although individual estimates of ALI and DLI were nonsignificant. These data show that BSSS(R) became earlier and BSCB1(R) became later with selection. Regardless of genetic drift effects, selection tended to decrease flowering dates in BSSS(R) but increase flowering dates in BSCB1(R) population.

Direct effects of selection (ALI + DLI + DLII') were significant for silking date in BSSS(R) and for pollen date in BSSS(R) and BSCB1(R). BSSS(R) when crossed to BSCB1(R) contributes earliness in flowering dates in population cross. On the contrary, BSCB1(R) when crossed to BSSS(R) tended to delay the flowering dates in the population cross. The estimated direct response in silking dates for the interpopulation crosses showed a significant decrease in days to silk of -0.279 ± 0.058

days cycle^{-1}. No significant difference was observed for the direct response in pollen dates for the interpopulation crosses. Effects of genetic drift increased days to silk and pollen shedding in BSSS(R) but did not significantly change either character in BSCB1(R).

The estimate of heterosis (HII') was significant for pollen date suggesting the diversity of allelic frequencies between BSSS(R)C0 and BSCB1(R)C0. The estimate of HII' for silking date was not significant. Because the estimate of DLII' for silking date in BSCB1(R) was significant, lack of a significant estimate of HII' for silking date can not be interpreted as an absence of genetic diversity for this trait in the base populations. The model may not be able to detect the small difference between initial allelic frequencies for this trait. Significant estimates of HQII' for both traits confirm that there were changes in allelic frequencies of loci affecting silking and pollen dates in both populations.

CONCLUSIONS

The genetic changes due to contributions of additive and dominance effects which caused changes in performance of the traits over cycles of selection were evaluated using genetic parameters from Smith's (1983) model. Performance of the original populations for grain yield, ear height, plant height, silking date, and pollen date were largely controlled by additive effects although dominance effects made some contributions to the traits. Grain moisture in the original populations was particularly controlled by additive effects while dominance effects appear to be more important in performance of stalk lodging in the original populations.

Increases in grain yield with cycles of selection resulted from changes in frequency of alleles involving both additive and dominance effects in BSSS(R) and primarily dominance effects in BSCB1(R). Significant estimates of DQI indicate that effects of selection in improving grain yield in the populations per se were confounded with the effects of genetic drift. After adjusting for the effects of genetic drift, the indirect response in both populations were similar to the direct response in BSSS(R) x BSCB1(R) interpopulation crosses. It was found that the rates of reduction in grain yield due to the effects of genetic drift were similar for both populations. Genetic drift was also important in decreasing ear height in BSCB1(R) and plant height in both populations, and increasing days to flowering in BSSS(R).

The responses for most evaluated traits were in the desired direction and consistent with the previous report (Keeratinijakal and

Lamkey, 1990). However, improvement of root lodging in the populations reported in the previous study can not be confirmed from results obtained from Smith's model.

It is evident from this study that inbreeding due to finite population size was responsible for the lack of improvement in the observed grain yield of the populations. The accumulated inbreeding would depress mean performance and reduce the amount of genetic variance in the populations. Thus, the maximum potential of the populations may never be realized. The inbreeding associated with genetic drift may not be avoided in the RRS program because a limited number of individuals is selected for recombination. The change to intermating 20 selected lines rather than 10 selected lines for the last three cycles in this RRS program was done to reduce cumulative effects of genetic drift. The sample size of 20 lines for recombination is considered a minimum effective size and would result in some level of inbreeding (Robertson, 1960; Hallauer and Miranda, 1988). To minimize the inbreeding effects as much as possible, more than 20 lines should be intermated in each cycle of selection. However, more testcross progenies would also be needed for evaluation to maintain the same selection intensity.

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GENERAL DISCUSSION AND CONCLUSIONS

This study was conducted to evaluate the response after 11 cycles of RRS in BSSS(R) and BSCB1(R) populations. The results indicated that RRS effectively increased the mean grain yield of the BSSS(R)Cn x BSCB1(R)Cn population crosses at the rate of 6.95% cycle^{-1}. A lower rate of response was observed in BSCB1(R)Cn (1.94% cycle^{-1}), but no significant change was detected in the BSSS(R)Cn.

Although not statistically significant in all instances, selection caused favorable changes in other agronomic traits. No major changes were observed after selection for grain moisture. Selection tended to decrease both root and stalk lodging for populations and interpopulation crosses. Increased response to selection after cycle 4 for stalk lodging appeared to result from the use of machine-harvested yield rather than hand-harvested yield as a selection criteria and the screening of S_1 plants before making testcrosses. The improved populations of BSSS(R) and BSCB1(R) tended to have reduced ear and plant height while an increasing trend occurred in the population crosses. The reduction in ear and plant height in the populations resulted from effects of inbreeding due to small population size. Days to flowering initially increased in BSCB1(R) but decreased in BSSS(R)Cn. These changes were attributed to selection of plants in each population to produce the testcross progenies, because BSCB1(R)C0 was about six days earlier flowering than BSSS(R)C0.

According to the estimated genetic parameters from Smith's model, RRS has increased the frequency of favorable alleles affecting grain

yield in the parental populations. Gain for grain yield in BSSS(R) was caused by changes in frequency of alleles with additive and dominance effects, but only alleles with dominance effects were important in BSCB1(R). However, significant effects of genetic drift were observed in BSSS(R)Cn and BSCB1(R)Cn, explaining the lack of responses observed in mean grain yield of both populations. The estimated indirect responses in both populations after adjusting for effects of genetic drift were similar to the estimated direct response in the interpopulation cross.

Genetic drift may not be avoided in a recurrent selection program because of the limited number of progenies recombined each cycle. Three procedures could be used to minimize the inbreeding effects due to finite population size. First is to use more progenies for recombination in each cycle. The second is to outcross each population to an unrelated elite population after several cycles of selection. The third is to outcross each population, after a few cycles of selection, to its corresponding germplasm reserve and backcross to the population (Sprague and Eberhart, 1977). The second and third procedures may not be considered if the study of long-term effects in the closed populations of the RRS program is of interest. The use of a larger population size would reduce inbreeding, but it would also reduce the selection intensity. Thus, evaluation of large number of testcross progenies would also be necessary to maintain the appropriate selection intensity.

The increases in grain yield of the crosses of BSSS(R)Cn and BSCB1(R)Cn with inbred testers suggested that RRS was effective in improving general as well as specific combining ability of the

populations. Effects of selection and genetic drift would be sufficient to create different allele frequencies between the populations and their related inbred testers which resulted in heterosis in the crosses.

Heterozygous loci involving grain yield have increased in the population crosses, as suggested by the increased heterosis and inbreeding depression in the population crosses. The increased grain yield heterosis in the interpopulation crosses resulted from selection for alleles at complementary loci in each population and fixation of different alleles at a locus in each population by genetic drift.

Because grain yield and other agronomic traits, especially standability of the interpopulation crosses, have been sufficiently improved in the RRS program, it is most likely that the crosses between lines derived from improved populations of BSSS(R) and BSCB1(R) would provide hybrids with high grain yield and satisfactory performance of agronomic traits. The improved combining ability of the populations per se would also ensure that the improved populations could be used as germplasm sources for extraction of inbred lines for use in applied breeding programs.

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APPENDIX

Table A1. Combined analysis of variance of the S_0 experiments over environments in 1988 and 1989 for eight traits

Source of variation	df	Mean squares: Grain: Yield	Grain: Moisture	Root lodging
ENVIRONMENTS	6[a]	683.55**	3780.19**	27753.19**
ENTRIES	102	38.96**	37.31**	158.98*
1) Group 1 (BSSS)	10	4.73**	9.07**	106.10
BSSS per se				
Linear	1	0.88	1.12	468.50*
Quadratic	1	3.18	7.25	13.73
BSSS(CO) x BSSS(Cn)				
Linear	1	38.69**	22.09**	29.90
Quadratic	1	0.29	0.10	0.07
Lack of fit	6	0.71	0.01	91.96
2) Group 2 (BSCB1)	10	8.21**	6.30*	199.81
BSCB1 per se				
Linear	1	5.25*	2.27	1154.91**
Quadratic	1	0.25	3.07	147.56
BSCB1(CO) x BSCB1(Cn)				
Linear	1	68.10**	0.04	434.58
Quadratic	1	0.62	3.12	7.06
Lack of fit	6	1.32	9.08**	42.34
3) Group 3 (BSSS x BSCB1)	14	27.49**	8.54**	89.59
BSSS(Cn) x BSCB1(Cn)				
Linear	1	282.90**	18.81*	0.98
Quadratic	1	1.75	4.97	42.02
BSSS(CO) x BSCB1(Cn)				
Linear	1	29.98**	4.41	207.97
Quadratic	1	1.86	8.42	0.44
BSSS(Cn) x BSCB1(CO)				
Linear	1	47.87**	0.06	197.67
Quadratic	1	0.95	18.87*	0.85
Lack of fit	8	2.44*	8.00**	100.54

[a]Degrees of freedom is 4 for ear and plant height and 1 for silking and pollen date.

*,**Significant at the 0.05 and 0.01 probability levels, respectively.

Mean squares				
Stalk	Height		Date	
lodging	Ear	Plant	Silking	Pollen
23664.61**	78290.61**	165909.22**	5213.11**	4251.96**
1086.86**	739.90**	1314.62**	14.51**	12.43**
180.95	317.86**	332.46**	12.82**	5.21**
619.47*	2173.81**	318.45	68.89**	6.11*
206.36	205.51	67.31	3.13	13.62**
392.64	0.16	374.96*	40.80**	13.30**
4.77	298.58*	562.39*	3.36	5.92*
97.71	83.42	333.57**	2.01	2.20
3277.98**	379.45**	645.67**	9.07**	13.59**
26227.00**	2975.77**	2827.51**	33.66**	79.80**
57.97	113.01	126.75	39.41**	30.79**
5210.22**	71.92	2343.28**	2.59	1.77
14.41	255.52*	433.90*	4.28	7.83**
211.66	63.05	120.88	1.79	2.63**
1072.09**	106.21*	813.47**	14.12**	5.36**
7192.00**	408.01**	6393.73**	29.35**	0.18
1149.60**	0.33	3.12	1.29	0.02
3524.92**	384.32**	864.30**	31.81**	32.09**
75.00	118.57	187.94	3.41	2.68
723.62**	3.36	1661.83**	112.99**	21.95**
65.87	65.09	0.36	3.97	4.40
284.79**	63.41	284.66**	1.86	1.71

Table A1. (Continued)

Source of variation	df	Mean squares: Grain Yield	Grain Moisture	Root lodging
4) Testcrosses	27	11.12**	25.48**	122.18
BSSS testcrosses	13	7.71**	7.09**	49.39
Tester B73	6	6.63*	6.30	86.92
Linear	1	21.13**	2.02	0.40
Quadratic	1	1.99	8.40	95.34
Lack of fit	4	3.26*	6.85	106.44
Tester Mo17	6	8.96**	8.87**	18.76
Linear	1	40.15**	25.81**	4.62
Quadratic	1	5.67*	0.01	28.71
Lack of fit	4	1.97	6.85	19.80
Tester B73 vs Tester Mo17	1	10.30**	1.22	7.94
BSCB1 testcrosses	13	15.39**	8.90**	87.03
Tester B73	6	8.40**	1.17	49.38
Linear	1	47.44**	2.02	9.77
Quadratic	1	1.95	2.02	17.51
Lack of fit	4	0.25	0.74	67.24
Tester Mo17	6	11.06**	3.67	61.74
Linear	1	62.48**	7.48	45.44
Quadratic	1	3.57	2.21	52.65
Lack of fit	4	0.32	3.08	68.08
Tester B73 vs Tester Mo17	1	83.25**	86.64**	464.64*
BSSS TC vs BSCB1 TC	1	0.04	480.07**	1525.51**
5) Check populations	13	46.54**	27.08**	200.54
6) Remainder	28	91.23**	89.01**	214.17**
ENTRY x ENVIRONMENT	---[b]	1.22** (612)	2.99** (612)	120.43** (612)
POOLED ERROR	---[b]	0.63 (1316)	1.88 (1376)	73.43 (1346)

[b]Degrees of freedom for the entry x environment and the pooled errors are shown in parentheses under each trait.

Mean squares				
Stalk	Height		Date	
lodging	Ear	Plant	Silking	Pollen
237.91**	147.66**	596.59**	4.17**	4.33**
182.57*	83.26	235.71**	7.09**	4.47**
87.49	122.94*	318.07**	9.39**	2.09
129.55	2.09	0.06	49.70**	10.82**
22.03	30.78	0.86	6.08	0.55
93.34	176.20*	476.88**	0.14	0.29
58.43	46.02	189.47	5.80**	0.45
173.96	19.52	526.94*	29.78**	0.39
2.31	82.19	6.44	2.00	1.85
43.58	43.61	150.86	0.75	0.11
1497.84**	68.57	18.90	1.10	42.86**
296.60**	219.78**	997.54**	1.15	2.35*
350.14**	33.09	161.19	0.92	2.04
1773.18**	29.70	816.24**	0.43	6.68*
28.41	62.90	100.65	2.15	4.42
74.80	26.49	12.55	0.73	0.28
217.68	100.52	131.34	1.57	1.04
412.97*	192.44	360.68*	3.25	0.13
59.93	238.26*	28.38	3.83	3.80
208.28	43.11	99.75	0.58	0.58
448.94*	2055.47**	11212.81**	0.07	12.04**
194.41	47.34	75.86	5.36	28.34**
1374.79**	1059.32**	1477.39**	37.34**	30.29**
1320.19**	1758.99**	2771.69**	16.62**	17.65**
103.98**	53.24**	90.42**	1.80**	1.15**
(612)	(408)	(408)	(102)	(102)
67.03	28.36	50.72	0.87	0.66
(1316)	(1376)	(1406)	(376)	(376)

Table A2. Combined analysis of variance of the S_1 experiments over environments in 1988 and 1989 for eight traits

Source of variation	df	Mean squares			
		Grain		Lodging	
		Yield	Moisture	Root	Stalk
ENVIRONMENT	6	56.48**	514.96**	2276.34**	984.45**
REP (ENV)	14	0.86	4.21	571.99**	66.69
ENTRY	13	2.10**	54.98**	126.78	729.95**
1) BSSS(R)	6	2.73**	9.51**	40.45	124.17
Linear	1	13.28**	2.29	88.89	399.19*
Quadratic	1	0.29	0.18	30.44	38.37
Lack of fit	4	0.71	13.65**	30.84	76.86
2) BSCB1(R)	6	0.48	4.39	76.21	1389.83**
Linear	1	0.71	8.03	115.50	7800.70**
Quadratic	1	0.07	2.68	252.08	156.62
Lack of fit	4	0.53	3.91	22.42	95.42
3) BSSS(R) vs BSCB1(R)	1	8.35**	624.24**	960.14**	328.56*
ENTRY x ENVIRONMENT	78	0.60**	2.64	85.91**	62.44**
POOLED ERROR	182	0.24	2.41	37.28	30.52

*,**Significant at the 0.05 and 0.01 probability levels, respectively.

Table A3. Combined analysis of variance of the S_1 experiments over locations in 1989 for eight traits

Source of variation	df	Mean squares			
		Grain		Lodging	
		Yield	Moisture	Root	Stalk
ENVIRONMENT	2	71.66**	891.06**	6624.95**	467.12**
REP (ENV)	6	3.58**	5.15	1749.68**	180.49*
ENTRY	20	6.43**	25.08**	175.48	252.71**
BSSS(R)	6	4.94**	6.97*	79.60	73.01
BSCB1(R)	6	0.56	1.41	198.42	591.27**
BSSS(R) vs BSCB1(R)	6	5.03**	3.68	44.97	171.33*
Linear	1	25.69**	18.09**	188.22	664.40**
Quadratic	1	3.21**	0.16	72.27	4.36
Lack of fit	4	0.32	0.96	2.33	89.80
Remainder	2	32.71**	214.62**	785.83**	20.27**
ENTRY x ENVIRONMENT	40	0.39	2.30*	129.49**	69.56**
POOLED ERROR	120	0.33	1.45	67.47	34.00

[a]One environment for silking and pollen date.

*,**Significant at the 0.05 and 0.01 probability levels, respectively.

Mean squares Height			Mean squares Date	
Ear	Plant	df	Silking	Pollen
5936.99**	9451.86**	--[a]		
10.22	136.21	2	12.49**	13.19**
414.25**	1258.96**	20	4.42**	6.54**
36.53	391.79**	6	8.32**	3.78**
89.96	203.96*	6	2.98**	2.22
84.49	653.56**	6	0.39	2.21
292.73*	2872.82**	1	0.57	8.73**
6.00	25.13	1	0.41	0.08
52.06	255.86*	1	0.34	1.11
3509.56**	8841.67**	2	9.13**	40.77**
49.94	71.18			
40.27	65.14	40	0.54	1.11

Table A4. X matrix used for estimating the genetic parameters of the Smith (1983) model

Entry	Coefficients					
	AOI	AOI'	DOI	DOI'	ALI	ALI'
BSSS(R)C0	1	0	2	0	0	0
BSSS(R)C4	1	0	2	0	8	0
BSSS(R)C7	1	0	2	0	14	0
BSSS(R)C8	1	0	2	0	16	0
BSSS(R)C9	1	0	2	0	18	0
BSSS(R)C10	1	0	2	0	20	0
BSSS(R)C11	1	0	2	0	22	0
BSCB1(R)C0	0	1	0	2	0	0
BSCB1(R)C4	0	1	0	2	0	8
BSCB1(R)C7	0	1	0	2	0	14
BSCB1(R)C8	0	1	0	2	0	16
BSCB1(R)C9	0	1	0	2	0	18
BSCB1(R)C10	0	1	0	2	0	20
BSCB1(R)C11	0	1	0	2	0	22
BSSS(R)C0 x BSSS(R)C4	1	0	2	0	4	0
BSSS(R)C0 x BSSS(R)C7	1	0	2	0	7	0
BSSS(R)C0 x BSSS(R)C9	1	0	2	0	9	0
BSSS(R)C0 x BSSS(R)C11	1	0	2	0	11	0
BSSS(R)C4 x BSSS(R)C7	1	0	2	0	11	0
BSSS(R)C4 x BSSS(R)C9	1	0	2	0	13	0
BSSS(R)C4 x BSSS(R)C11	1	0	2	0	15	0
BSSS(R)C7 x BSSS(R)C9	1	0	2	0	16	0
BSSS(R)C7 x BSSS(R)C11	1	0	2	0	18	0
BSSS(R)C9 x BSSS(R)C11	1	0	2	0	20	0
BSCB1(R)C0 x BSCB1(R)C4	0	1	0	2	0	4
BSCB1(R)C0 x BSCB1(R)C7	0	1	0	2	0	7
BSCB1(R)C0 x BSCB1(R)C9	0	1	0	2	0	9
BSCB1(R)C0 x BSCB1(R)C11	0	1	0	2	0	11
BSCB1(R)C4 x BSCB1(R)C7	0	1	0	2	0	11
BSCB1(R)C4 x BSCB1(R)C9	0	1	0	2	0	13
BSCB1(R)C4 x BSCB1(R)C11	0	1	0	2	0	15
BSCB1(R)C7 x BSCB1(R)C9	0	1	0	2	0	16
BSCB1(R)C7 x BSCB1(R)C11	0	1	0	2	0	18
BSCB1(R)C9 x BSCB1(R)C11	0	1	0	2	0	20
BSSS(R)C0 x BSCB1(R)C0	0.5	0.5	1	1	0	0
BSSS(R)C4 x BSCB1(R)C4	0.5	0.5	1	1	4	4
BSSS(R)C7 x BSCB1(R)C7	0.5	0.5	1	1	7	7
BSSS(R)C8 x BSCB1(R)C8	0.5	0.5	1	1	8	8
BSSS(R)C9 x BSCB1(R)C9	0.5	0.5	1	1	9	9
BSSS(R)C10 x BSCB1(R)C10	0.5	0.5	1	1	10	10
BSSS(R)C11 x BSCB1(R)C11	0.5	0.5	1	1	11	11

Coefficients							
DLI	DLI'	DQI	DQI'	DLII'	DLI'I	HII'	HQII'
0	0	0	0	0	0	0	0
8	0	32	0	0	0	0	0
14	0	98	0	0	0	0	0
16	0	128	0	0	0	0	0
18	0	162	0	0	0	0	0
20	0	200	0	0	0	0	0
22	0	242	0	0	0	0	0
0	0	0	0	0	0	0	0
0	8	0	32	0	0	0	0
0	14	0	98	0	0	0	0
0	16	0	128	0	0	0	0
0	18	0	162	0	0	0	0
0	20	0	200	0	0	0	0
0	22	0	242	0	0	0	0
4	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0
11	0	56	0	0	0	0	0
13	0	72	0	0	0	0	0
15	0	88	0	0	0	0	0
16	0	126	0	0	0	0	0
18	0	154	0	0	0	0	0
20	0	198	0	0	0	0	0
0	4	0	0	0	0	0	0
0	7	0	0	0	0	0	0
0	9	0	0	0	0	0	0
0	11	0	0	0	0	0	0
0	11	0	56	0	0	0	0
0	13	0	72	0	0	0	0
0	15	0	88	0	0	0	0
0	16	0	126	0	0	0	0
0	18	0	154	0	0	0	0
0	20	0	198	0	0	0	0
0	0	0	0	0	0	0	0
4	4	0	0	8	8	2	32
7	7	0	0	14	14	2	98
8	8	0	0	16	16	2	128
9	9	0	0	18	18	2	162
10	10	0	0	20	20	2	200
11	11	0	0	22	22	2	242

Table A4. (Continued)

Entry	Coefficients					
	AOI	AOI'	DOI	DOI'	ALI	ALI'
BSSS(R)C0 x BSCB1(R)C4	0.5	0.5	1	1	0	4
BSSS(R)C0 x BSCB1(R)C7	0.5	0.5	1	1	0	7
BSSS(R)C0 x BSCB1(R)C9	0.5	0.5	1	1	0	9
BSSS(R)C0 x BSCB1(R)C11	0.5	0.5	1	1	0	11
BSSS(R)C4 x BSCB1(R)C0	0.5	0.5	1	1	4	0
BSSS(R)C4 x BSCB1(R)C7	0.5	0.5	1	1	4	7
BSSS(R)C4 x BSCB1(R)C9	0.5	0.5	1	1	4	9
BSSS(R)C4 x BSCB1(R)C11	0.5	0.5	1	1	4	11
BSSS(R)C7 x BSCB1(R)C0	0.5	0.5	1	1	7	0
BSSS(R)C7 x BSCB1(R)C4	0.5	0.5	1	1	7	4
BSSS(R)C7 x BSCB1(R)C9	0.5	0.5	1	1	7	9
BSSS(R)C7 x BSCB1(R)C11	0.5	0.5	1	1	7	11
BSSS(R)C9 x BSCB1(R)C0	0.5	0.5	1	1	9	0
BSSS(R)C9 x BSCB1(R)C4	0.5	0.5	1	1	9	4
BSSS(R)C9 x BSCB1(R)C7	0.5	0.5	1	1	9	7
BSSS(R)C9 x BSCB1(R)C11	0.5	0.5	1	1	9	11
BSSS(R)C11 x BSCB1(R)C0	0.5	0.5	1	1	11	0
BSSS(R)C11 x BSCB1(R)C4	0.5	0.5	1	1	11	4
BSSS(R)C11 x BSCB1(R)C7	0.5	0.5	1	1	11	7
BSSS(R)C11 x BSCB1(R)C9	0.5	0.5	1	1	11	9
[BSSS(R)C0] S[a]	1	0	1	0	0	0
[BSSS(R)C4] S	1	0	1	0	8	0
[BSSS(R)C7] S	1	0	1	0	14	0
[BSSS(R)C8] S	1	0	1	0	16	0
[BSSS(R)C9] S	1	0	1	0	18	0
[BSSS(R)C10] S	1	0	1	0	20	0
[BSSS(R)C11] S	1	0	1	0	22	0
[BSCB1(R)C0] S	0	1	0	1	0	0
[BSCB1(R)C4] S	0	1	0	1	0	8
[BSCB1(R)C7] S	0	1	0	1	0	14
[BSCB1(R)C8] S	0	1	0	1	0	16
[BSCB1(R)C9] S	0	1	0	1	0	18
[BSCB1(R)C10] S	0	1	0	1	0	20
[BSCB1(R)C11] S	0	1	0	1	0	22
[BSSS(R)C0 x BSCB1(R)C0] S	0.5	0.5	0.5	0.5	0	0
[BSSS(R)C4 x BSCB1(R)C4] S	0.5	0.5	0.5	0.5	4	4
[BSSS(R)C7 x BSCB1(R)C7] S	0.5	0.5	0.5	0.5	7	7
[BSSS(R)C8 x BSCB1(R)C8] S	0.5	0.5	0.5	0.5	8	8
[BSSS(R)C9 x BSCB1(R)C9] S	0.5	0.5	0.5	0.5	9	9
[BSSS(R)C10 x BSCB1(R)C10] S	0.5	0.5	0.5	0.5	10	10
[BSSS(R)C11 x BSCB1(R)C11] S	0.5	0.5	0.5	0.5	11	11

[a] S_1 generation.

Coefficients							
DLI	DLI'	DQI	DQI'	DLII'	DLI'I	HII'	HQII'
0	4	0	0	0	8	2	0
0	7	0	0	0	14	2	0
0	9	0	0	0	18	2	0
0	11	0	0	0	22	2	0
4	0	0	0	8	0	2	0
4	7	0	0	8	14	2	56
4	9	0	0	8	18	2	72
4	11	0	0	8	22	2	88
7	0	0	0	14	0	2	0
7	4	0	0	14	8	2	56
7	9	0	0	14	18	2	126
7	11	0	0	14	22	2	154
9	0	0	0	18	0	2	0
9	4	0	0	18	8	2	72
9	7	0	0	18	14	2	126
9	11	0	0	18	22	2	198
11	0	0	0	22	0	2	0
11	4	0	0	22	8	2	88
11	7	0	0	22	14	2	154
11	9	0	0	22	18	2	198
0	0	0	0	0	0	0	0
4	0	16	0	0	0	0	0
7	0	49	0	0	0	0	0
8	0	64	0	0	0	0	0
9	0	81	0	0	0	0	0
10	0	100	0	0	0	0	0
11	0	121	0	0	0	0	0
0	0	0	0	0	0	0	0
0	4	0	16	0	0	0	0
0	7	0	49	0	0	0	0
0	8	0	64	0	0	0	0
0	9	0	81	0	0	0	0
0	10	0	100	0	0	0	0
0	11	0	121	0	0	0	0
0	0	0	0	0	0	1	0
2	2	0	0	4	4	1	16
3.5	3.5	0	0	7	7	1	49
4	4	0	0	8	8	1	64
4.5	4.5	0	0	9	9	1	81
5	5	0	0	10	10	1	100
5.5	5.5	0	0	11	11	1	121